Flow preferences of benthic macroinvertebrates in three Scottish Rivers

by

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This thesis is dedicated to my parents.

Abstract

Scottish freshwaters have been described as a national resource of international significance. The high quality of Scotland's lotic systems is integral to the formation of this view. The research presented here aims to provide an insight into the interaction between benthic invertebrates and their hydraulic habitat within some of Scotland's lotic systems. A further aim of this project is that this information presented here will aid the design of river rehabilitation and management schemes thereby helping maintain the integrity of the opening statement.

There is a large amount of literature existing which addresses the interactions between benthic invertebrates and flow parameters; substrate type, vegetation, velocity, depth and near bed stresses. However significant gaps remain in our understanding, particularly at the level of individual taxa preferences. Furthermore, little work has been done in Scotland. To address these gap in the data the distribution of macro-invertebrates in relation to flow parameters were assessed for three rivers representative of highland (River Etive), central belt (Blane Water) and borders rivers (Duneaton Water).

The importance of deep and shallow reaches as habitat units for benthic invertebrates was analysed and the methods for categorising reaches into riffles, runs and pools assessed. The analysis showed that at the sites examined differences between invertebrate community in deep and shallow reaches were minimal and limited to the preferences of a number of key species. Categorising reaches into riffles, runs and pools on purely visual grounds was insufficient and some measures of velocity and depth are required if the work is to be used for between site comparisons.

Benthic invertebrates did show preferences for flow parameters. At the physical scale examined (Surber sample) community structure was influenced in a limited manner by flow parameters; velocity and depth wre the most important. A gradient from erosional to depositional conditions was observed at two of the sites.

Limitations of Instream Flow Incremental Methodology (IFIM) as applied to benthic invertebrate habitat identification were identified. Estimates of near bed flow parameters based on point measurements of velocity profiles to samples collected at the scale of Surber samples do not explain any additional variation in the distribution of benthic invertebrates. Analysis of individual flow preferences of macroinvertebrates suggest that to identify flow preference curves, an aim of IFIM, finer scale habitat measurements are needed.

Laboratory experiments were carried out to identify the upper velocity tolerances of some benthic invertebrates; Tipulidae and *Gammarus pulex*. The results show that individuals were flexible in their responses to high velocities. What constituted 'high' velocity was taxa specific.

Benthic invertebrate community structure was investigated in areas of the Blane Water vegetated with *Callitriche instagnalis*. Submerged vegetated patches supported a greater abundance of invertebrates than bare substrate. The hydraulic habitat of the macrophyte stands was more diverse than that of bare substrate with higher velocities occurring on the outside of the macrophyte stands than on the bare substrate. Simuliidae dominated the outside of the stands, the area exposed to the highest velocities. The invertebrate community on the outside of the plant stands was less equitable than that found at the root-substrate interface. It is suggested that macrophytes can be used as a tool in the rehabilitation of hydraulic habitat for benthic invertebrates in Scottish rivers.

The importance of these results are discussed in the context of river rehabilitation and our ecological understanding of benthic invertebrate community structure.

CONTENTS

Declaration

I declare that the work 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 for any other degree.

Matthew ÓHare
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Chapter 1:General Introduction

The main aim of this project was to improve the scientific knowledge base of benthic invertebrate - environment interactions in streams, to assist the better design of river rehabilitation and management schemes. The basic question to answer is whether or not instream flow preferences of benthic invertebrates can be identified. There is a large body of work addressing various aspects of this question but it remains to a large extent unanswered especially in a quantified manner. The thesis chapters outlined at the end of the introduction, show a progression from field surveys to laboratory experiments, where initial measurements made in the field are tested in the laboratory. Finally macrophytes, which provide a velocity gradient are examined as macroinvertebrate habitat. Part of the aim of this work is to follow the ecohydrological approach, that is the combining of ecology and hydrology to better improve our understanding and management of freshwaters. In its infancy, this discipline still suffers from a lack of basic definitions hampering work. The first sections of this general introduction cover the basic biology and physical structure of rivers, partly for general information but also to clarify some of these basic definitions, and paradigms as I perceive them. A more specific introduction to the work follows the general sections.

General background

1.1 The biology of flowing water benthic macroinvertebrates

Macroinvertebrates are a practical grouping of freshwater organisms, simply defined as invertebrates occurring in or on (or associated with) the substrate, and visible to the naked eye. Meiofauna which are invisible to the naked eye are often the more species rich and abundant of the two categories of benthic fauna but remain relatively neglected (Poff *et al.* 1993; Ward *et al.* 1998). Being wholly dependent on size, membership of the two groups is not exclusive, a situation well illustrated by the Chironomidae which can occupy both groupings during their larval stage. Constituting a number of phyla the macro-invertebrates exhibit a range of life histories. The majority of the phyla spend their entire life cycles in the lotic system; Crustacea, Mollusca, Annelida and Platyhelminthes[1].[2]

The remaining major grouping, the Insecta spend only their juvenile stages in the system, although among some groups there are exceptions; the Coleoptera and the Hemiptera. The insects are the most extensively studied of the benthic invertebrates and several texts are exclusively devoted to them (Merrit & Cummins 1979; Williams & Feltmate 1994).

Most of the insects are univoltine or bivoltine but some species can take two years to mature. It is very rare for animals to take longer than two years to mature in lotic systems (Williams & Feltmate 1994). Adult emergence for the Ephemeroptera and some members of the other groups is famously synchronised but time spent on the wing can be highly variable. In the Trichoptera some taxa can spend the entire summer on the wing waiting to reproduce. From a number of studies it clear is that growth rates are plastic, and may reflect ambient temperature and food availability or other environmental variables (Petts & Bickerton 1994; Webb & Walling 1993). As the fecundity of these animals is almost

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[1] Other phyla do occur in running freshwater but were not encountered during this study. A checklist of the north European taxa is given in (Fitter & Manuel 1994). For simplicity the taxonomic hierarchy used in that publication is used throughout the thesis and is not a reflection of the author's views on the taxonomic structure of the Arthropoda which remains unresolved and controversial (Brusca & Brusca 1990).

[2] There are a number of exceptions among the Gastropoda; it has been stated that it is difficult to distinguish between aquatic and terrestrial forms. (Macan 1977). The sub-class Euthyneura are exclusively represented by the order Pulmonata in this study are air breathers and can exist in quite dry conditions. Of their members the species most frequently encountered in the study is *Ancylus fluviatilis* which does not need to breath air and is wholly aquatic (Clegg 1952)!

exclusively dependent on juvenile feeding - see below - environmental conditions during the juvenile stage are of the utmost importance.

Few adult aquatic insects have been observed feeding but some Trichoptera and Chironomidae adults have been observed sipping nectar, Homopteran honeydew and sugar water in the wild and captivity (Armitage *et al.* 1995; Malicky 1981). The contribution to the animals' overall fecundity is likely to be slight as these food sources contain little more than carbohydrates (Svensson 1972). Dragonflies feed throughout their adult lives, but were not encountered in the work presented here (Hammond & Merrit 1983; Miller 1987). Some Plecoptera (Nemouridae) need to feed before they can lay eggs, but even in these cases the majority of the adult biomass must come from larval feeding (Hynes 1976). Diptera are the major exception, with fecundity closely related to blood feeding across some of the families. In general though, investment by invertebrate adults in individual young is limited.

Oviposition strategy can have a strong influence on the distribution of the juvenile forms on the substrate and may, in the case of insects and depending on species, be a product of parental habitat use rather than larval preference (Harrison & Hildrew 1998). This is more likely in lentic systems than lotic where there are fewer modes of larval dispersal. The Gastropoda encountered in this study produce their eggs in jellied masses on rocks and other submerged substrata (Clegg 1952) and in the case of *Potamopyrgus jenkinsi* by asexual means (Maitland 1990). Among the Annelida, egg laying also occurs; the eggs being laid in capsules (Brinkhurst 1963). In the insects, parental care appears limited to oviposition. Eggs are laid in the water under stones (*Baetis*) on the water surface (*Ephemerella ignita)* or on bankside vegetation (some Trichoptera).

The numbers of eggs produced by all members of the aquatic taxa shows high degrees of intra and interspecies variation (Macan 1963), hinting at a range of reproductive strategies. Sexual reproduction appears to be the norm among aquatic insects but asexual reproduction in the Chironomidae and Ephemeroptera has been recorded (Armitage *et al.* 1995).

The only aquatic groups which do show some maternal care are the amphipod and isopod crustaceans which brood their young (Clegg 1952). It has recently been shown that the amphipod *Crangonyx pseudogracilis* also actively cares for their broods by flexing their bodies which alters the microhabitat of their brood pouches (Dick *et al.* 1998).

Although fundamental to our understanding of lotic ecosystems, little detailed work has been done on the dispersal of aquatic insects during the adult phase. Work on the genetic variability between populations of the Trichoptera in Australia indicate that there can be a much greater transfer of genetic material over large geographic areas than had previously been believed (Hughes *et al.* 1998)[3]. Aquatic insects occurring in a river stretch can be viewed as members of metapopulations, where the entire population may range in spatial occupation from a single island to the entire globe. Aquatic insects are thereby, potentially resilient to localised disturbance of lotic systems as long as their particular habitat patch continues to exist after the disturbance event and can be colonised by animals from

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[3] Research on Plecoptera showed distinct differences between streams suggesting that they do not disperse to the same extent as the Trichoptera of the other study (Hughes *et al.* 1999).

unaffected sites, e.g., if aquatic insects are subject to metapopoulation dynamics (Hanski 1994 & Levins 1969).

Dispersal between non-contiguous river systems is particularly difficult to assess for non-insect taxa which have no aerial phase. The rate of dispersal of invasive Crustacea (*Crangonyx pseudogracilis*) and Mollusca (*Potamopyrgus jenkinsi*) in the UK has been impressive, with both invaders now found throughout the country, less than one hundred and twenty years after being first recorded (Maitland 1990[4], Dick *et al.* 1997). Whether this was purely mediated by humans or reflects a natural ability to disperse between systems is difficult to determine at present. In the case of *Crangonyx* there is good evidence that the animal has moved between different catchments via the canal network although this is not always the case. It is likely that humans have influenced the dispersal, in the case of many fish species (Adams & Maitland 1998) and zebra mussels (Buchan & Padilla 1999). Future genetic work species and systems not heavily influenced by humans would help determine the degree of isolation of populations of these groups.

Once hatched benthic invertebrates find themselves near the base of the food chain, usually as primary consumers or detritivores, although some taxa are predatory right from hatching, e.g. the Tanypodinae. Depending on food particle size and feeding mechanisms of benthic invertebrates, the taxa have been assigned to functional feeding groups (Cummins 1973). Initially derived for insects only, it is now applied to the entire benthos (Moss 1988). The primary distinction is between herbivory, detritivory and carnivory. Ephemeroptera are viewed as mainly collector gatherers feeding on Fine Particulate

Organic Matter (FPOM) and scrapers, Plecoptera as predators or feeding on Coarse Particulate Organic Matter (CPOM) shredders. Tipulidae and Chironomidae can be shredders, collector gatherers (filterers) or predators. The Simuliidae, the other dipteran family are filter-collectors (Hart & Latta 1986). The Trichoptera and Coleoptera occur in almost all of the categories (Williams & Feltmate 1994: after Cummins 1973). The gastropods are viewed as scrapers, the Annelida as predators or deposit feeders and the Amphipoda and Isopoda as scrapers or collectors. The degree to which these groupings are exclusive is less certain. *Gammarus pulex* have scraping mouth parts but can use these to predate other amphipods which in turn may reduce interspecific competition (Dick 1992; Dick *et al.* 1990).

The link between feeding groups, animal mobility and morphology is strong. It is clear that to be a filterer being located in areas of high velocity and on stable substrate is useful and requires special adaptations e.g. suckers or retreats from energy consuming flow conditions. For collector gatherers, mobility is important and the animal must be able to swim through the water or crawl through / across the substrate matrix. It suggests there is a link between species (identified using morphological characteristics) and how they exploit their physical habitat. The river bed is heterogeneous and it is postulated that these animals occupy different physical niches (areas of stream bed) depending on their functional feeding groups.

Some of the major benthic taxa of interest in this study have the ability to be either parasitic or commensal on other invertebrates, feeding groups not addressed in Cummin's

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[4] As a human food source invasive crayfish species are excluded from the example as the influence of man in their dispersal is well recorded and affords little room to speculate about natural mechanisms.
C. *pseudogracilis* is still largely absent from the Scottish highlands.

classification, (Cummins, 1973). Chironomidae appear best suited to this role and are usually commensal, but can be parasitic (Tokeshi 1993). There has been at least one record of a Trichopteran (Orthotrichia) larva parasitic on other Trichopteran pupae (Wells 1992). The Hirudinea are of course the most famously parasitic freshwater group but in the systems studied here some leech species are predators, feeding directly on invertebrates (Elliot & Mann 1979). Although it is felt that flowing water somewhat negates the impact of ecto and endo parasites they do occur on the freshwater benthos. Hickin (1967) reviews the epizoites and epiphytes found on Trichopteran larvae and includes a mite, *Atturus scaber* infesting *Goera pilosa* and protozoa on a range of other species. Disease in general, is an area that has received little attention but could have a profound effect on aquatic benthos distribution.

So potentially, predation, food availability, disturbance and physical habitat structure alteration can affect the instream distribution of invertebrates and are well researched (Boulton *et al.* 1992; Crowl & Schnell 1990; Crowl *et al.* 1997; Dahl & Greenberg 1996; Death 1996; Dudgeon 1991; Dudgeon 1993; Dudgeon & Chan 1992; Hansen *et al.* 1991). Before proceeding further it is necessary to describe the physical habitat of lotic systems indicating the limits and opportunities which they present to aquatic benthic invertebrates.

1.2 Lotic systems: Physical structure

This section gives a short review of the physicochemical nature and geomorphological structure of lotic systems. The section on the geomorphological structure of rivers and their substrates focuses on the subject of the thesis, instream flow conditions; the physical factors examined as possible environmental gradients for invertebrates.

1.2.1 Life, light, temperature & water chemistry

The basic requirements of almost all life: water, light, oxygen, carbon dioxide and nutrients are available in lotic systems (Hutchinson 1957; Hynes 1972). Light penetration in rivers is normally limited by the turbidity of the water and it is only in the lower reaches of rivers, or in very large systems that depth becomes a limiting factor (Hynes 1972). Turbidity is usually dependent on discharge mobilising small particulate matter, and high turbidity is therefore more frequent in winter when the temperature (in temperate rivers) is too cool for much plant growth and the number of hours of sunlight are few and less intense. Dissolved atmospheric gases are rarely limiting in running waters which are frequently completely saturated or super saturated with oxygen, nitrogen and carbon dioxide. Freshwater insects appear to be dependent on this high level of available oxygen. Lowering the percentage of dissolved oxygen even slightly can have significant effects on the health of rheophilic amphipods, Trichoptera, Simuliidae, Ephemeroptera and Plecoptera (Golubkov *et al.* 1992; Kiel & Frutiger 1997; Macan 1963; Nagell & Larshammar 1981). For some Trichoptera their cases facilitate oxygen uptake (Williams *et al.* 1987) possibly allowing them to live in areas with lower oxygen levels. The capacity to tolerate lower oxygen levels is observed across most of the groups and tends to be found mainly among burrowers.

Rain water contains varying amounts of dissolved elements. The nutrient content of the river water is primarily dependent on the underlying bedrock geology, modified (often substantially) by catchment land use and other anthropogenic factors. Land use, particularly intensive agriculture and urban centres, have a detrimental impact on the chemical quality of water which may have a direct effect on the resident invertebrates. In Scotland, surface drift which, when glacially derived, can be of different chemical composition to the underlying bed rock, also contributes to the water chemistry (Survey 1971; Survey 1977).

The osmotic potential of freshwater can obviously be variable for the same reason nutrient concentration is variable. Aquatic insects are know to be hypertonic relative to freshwater and are capable of withstanding the normal fluctuations in its osmotic potential. They are not capable of withstanding the essential potential of salt water concentrations and this is one of the reasons cited as limiting the lotic benthos to rivers and making it non-contiguous with the marine system[5]. Also it is one of the many reasons cited why aquatic invertebrates do not drift too far downstream.

Temperature in running freshwaters varies more rapidly than in standing waters. Superimposed on seasonal changes are diurnal cycles. Surface water streams reflect mean air temperature over their entire length although this may alter as one proceeds down a valley. Spring melt of snows (which would be likely to affect all the rivers studied in this work) may have temperatures below that of the mean air temperature for significant periods subsequent to melting. On average, the upper sources of a catchment system tend to be cooler than further down. Temperature can have a profound effect on larval growth and emergence in the aquatic insects, best studied of these is probably *Baetis* and temperature is likely to effect the development of non-insect taxa in a similar manner. see

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[5] It has been pointed out that of the freshwater insects some groups have members occurring in marine environments. The trichopteran *Philanisus plebeius* lives in intertidal rock pools but has an additional organ not present in freshwater species which helps retain water within its hypotonic body (Leader 1976). As such the argument that limited osmoregulatory systems prevented insect colonisation of salt water begin to weaken.

Williams & Feltmate (1994) for a review of the effects of temperature on aquatic insects. Feeding is rarely limited by temperature according to (Cummins 1973), but it can effect instream distribution (Guinand *et al.* 1994).

Lotic systems have all the ingredients for primary productivity to succeed. They also have another factor which to a greater or lesser extent excludes the growth of instream macrophytes. That is the constant movement of water which makes the rooting of plants not only difficult but, if they do succeed in rooting, subject to removal by flooding. The constant erosion of fine sediment also leaves little suitable rooting material, most usually found in the lower reaches of river systems with mosses on rocks as the only rooted plants in the upper reaches The macrophytes which do occur in rivers are adapted to this disturbed habitat and often grow in shapes suitable for minimising drag (Sand-Jensen & Mebus 1996). Phytoplankton are also often only found in the lower reaches of rivers: frequently a major source of primary productivity is algae encrusting on rocks. Filamentous algae also grow attached to the substrate and under suitable conditions, a mixture of Chironomidae, diatoms and other Protista grow among their strands to form mats termed 'Aufwuchs' (Hynes 1972). Allochthonous material accounts for a large proportion of the energy entering the system and the amount is closely linked to the structure of the drainage system.

1.2.2 Drainage networks and Channel Structure

The simplest hierarchy is that of stream size; those tributaries furthest upstream are smallest in width and, as they progress to the sea, they join forming increasingly larger channels of higher stream order. The idea of ordering streams is that of R.A. Horton (Hynes 1972). The instream structure of channels also changes with distance from their source. Higher up in the catchments slopes tend to be steep, quickly shedding water, creating an erosional environment dominated by large substrate elements which can form 'step and pool' sequences (Carling 1995). Further down the system, the rivers still contain a lot of energy but are now wider and begin to deposit and erode material in a sequential manner (Carling 1995). This leads to the riffle-pool structure where when discharge is high pools are scoured out and the material deposited further downstream forming an extended lip called a riffle (Clifford 1993). During low discharge, fine substrates deposit in the pool sections, but not to the same extent in the riffle areas. Although relatively stable, the riffle-pool system is a constantly shifting dynamic habitat (Carling 1995). In gravel bed rivers some stability is created by the formation of an armoured layer where, through successive minor increases in discharge, the bed becomes compacted and in some cases the substrate elements align their long axis with the direction of flow. The armoured layer allows the persistence of finer substrate below this top compacted layer which, if it was not present, would be eroded. These middle reaches are the subject of the work done in this study this thesis. There can also be a zone of low permeability below the river bed were the water is no longer saturated with oxygen (van't Woudt & Nicolle 1978).

The deposition of material sorts it into mixed aggregates of different sized substrate elements; cobble bars, riffles, pools etc. These are often viewed as microhabitats for macrobenthos (Brown & Brussock 1991) and this is one of the questions addressed in this thesis. As the landscape flattens, energy in the river dissipates and its ability to carry sediment becomes reduced, here fine sediments become deposited as the river meanders. The discharge down a river is seasonal, reflecting precipitation within its catchment. Such fluctuations that do occur are classed by their return period, once in one hundred, twenty, ten years etc. Related to their intensity is their capacity to move substrate and alter the channel; some rivers in Scotland frequently migrate across their flood plains as a result of large, intermittent floods (Smith & Lyle 1994), e.g. the River Feshie.

1.2.3 Scale of physical processes, implications for ecology

Climate and topography are obviously not the only factors important in fashioning a river system and to aid biologists understanding of these processes and their biological context they have been categorised in a hierarchy with a number of spatial and temporally scales. A biological hierarchy of processes has also been identified and linked to this physical hierarchy of factors. The simplest method of linking the two is where the temporal scale of a physical process is similar to that of a biological one e.g. at a scale of 10^7 years, megaform processes such as plate tectonics, climate change and eustatic change create drainage networks which are on the same temporal scale as regional species pulses and evolutionary differentiation. Each level in the hierarchy influences that below it. There are a number of external physical and geomorphological processes working over a range of time intervals which, with the physical size of the area effected, are designated as mega, macro, meso, and microform processes. Macroform processes include flood plain change and channel evolution affecting river segments and are on the same time scale as possibly short term localised extinctions and variations in the available habitat. Mesoform processes are listed as the influence of shear stress, sediment deposition and channel processes which effect reach pool/riffle systems - microhabitats and work over similar time periods as metapopulation and patch dynamics and probability refugia. Microform processes include annual flow fluctuations, scour and deposition working on fine scale patches and the same time / and physical scale as the continuous distribution of invertebrates.

1.3 Lotic systems:ecological interpretation

Ecology is the study of the abundance, diversity and distribution of living organisms in the environment (Begon *et al.* 1996). Factors intrinsic to the macrobenthos and the extrinsic or environmental factors affecting their ecology were reviewed earlier in the introduction. General theories which attempt to explain the mechanisms underlying the ecology of organisms are numerous and some have been applied to lotic systems. Others have been developed specifically for lotic systems and what follows is a review of some of these theories.

The River Continuum Concept which integrates the changing structure of the temperate riverine environment along its length postulates that the middle reaches of rivers support the greatest range of animals (Statzner & Higler 1985). Reaches near the river's source lack light and therefore depend on allochthonous material supporting mainly shredders and their predators. The main food sources in the lower reaches are resident plankton and large amounts of FPOM derived from upstream sources which favours collector species.

The middle reaches are intermediate in type between the other two and therefore support the most diverse community.[6]

The assumption of the previous paragraph was that animals have different habitat preferences and when the habitat is diverse, the community is too; it assumes the animals are occupying different niches. The Competitive Exclusion Principle states that 'complete competitors cannot co-exist'. So how do so many species live together without driving one another to the point of extinction? This question is addressed indirectly in this thesis by attempting to show that the animals present are using different ranges of the flow gradients present; that there is niche differentiation along these physical hydraulic axes.

There are numerous models to choose from which attempt to explain species richness: Crawley (1986) lists eight. Freshwater ecologists argue as to whether the community structure is in a state of dynamic equilibrium, and hence structured mainly by species interactions (Minshall *et al.* 1985), or whether the system is constantly being disturbed by physical forces and is in non-equilibrium flux thus allowing species richness to be maintained at high levels (Tokeshi 1994). Giller & Malmquist (1998) point out that a more pluralist approach is now being adopted by ecologists and although this is the case it is informative to briefly reviews the merits of the different approaches (see Williams & Feltmate (1994) for a full review).

Some of the biological models (e.g. Spatial heterogeneity and The Musical Chairs Models) are dependent on the habitat being patchy while the non-equilibrium models depend on the

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[6] The River Continuum Concept is based on a number of studies looking at the diversity of the benthos along river systems; these works include a study on the River Endrick, of which the Blane Water is one of the study sites used here. The River Endrick another of the sites would be viewed as rithron dominated and although a middle order stream is more upland in nature.

natural disturbance (flooding) of river systems. Both are particularly applicable to lotic systems which are believed to be both patchy and disturbed.

It is known that benthic invertebrates frequently have aggregated and patchy distributions. The link between physical patchiness and invertebrate distribution has been made for individual species and communities distributions (Elliot 1977). Patchy distributions of invertebrates in lotic systems are reported at a number of scales; between-stream, and at a finer scale in stream patches (Badcock 1976; Evans & Norris 1997). Instream conditions can cause patchy distributions of invertebrates at a between-stream scale (Rutt *et al.* 1989), but of interest in this study are in stream distributions of invertebrates caused by instream habitat patchiness. Riffles and pools have already been mentioned as patches but patches can also occur on a finer physical scale. (Minshall 1984) gives a comprehensive review of insect - substratum relationships in which he cites references to show that animals have preferences for particle size, particle mixture and particle density (Malmquist & Otto 1987). It has also been recorded that animals prefer different aspects of stones (Whetmore *et al.* 1990). Velocity and depth are important variables with patchy spatial distributions and can cause the distribution of macrobenthos to mirror this patchiness; some caddis avoid areas of the stream bed where they would have to expend energy to withstand shear stresses (Bacher & Waringer 1996).

In lotic systems, disturbance is thought to be a major factor, although what constitutes a natural disturbance for lotic invertebrates is hard to say. They can be redistributed by flood events but normally they recover quickly unless the flood is very severe (Koetsier & Bryan 1995; Matthaei *et al.* 1996). As invertebrates drift as a normal means of redistributing, mortality seems likely to be rarely caused by it and sub-lethal impacts the more likely result of most disturbance events.

The theories mentioned above tend to concentrate on one aspect of the environment (either biotic or abiotic) as the major determinant of community structure. In reality there are interactions between major habitat characteristics e.g. disturbance events are ameliorated by habitat patchiness (Lancaster & Hildrew 1993) and more patchy habitats are possibly most resilient (Death 1996). Patch type can also differentially increase or decrease the impact of a disturbance event, e.g. taxa associated with sandy sections were significantly reduced after logging disturbance, but those on rock covered substrate increased (Gurtz & Wallace 1984)

Competition for patches can be influenced by disturbance which complicates models such as the 'Musical Chairs Model' which does not take into account disturbance at all, e.g. some sessile benthic invertebrate species have been shown not to prefer the most stable patches (stones) as predicted but those of intermediate stability, hence manipulating the relative importance of competition for space (Malmquist & Otto 1987). When predation is factored in along with competition and physical factors the situation can get very complex (Hart 1992).

As the natural situation is so complex there has been a general consensus in lotic ecology that it is most important to describe the scale, both physical and temporal, at which processes (and models) are most likely to operate rather than concentrating on testing models alone (Hildrew & Giller 1994). The categorisation of processes at different scales was described in detail in section 1.2 and it has been shown that hydrological factors can act in a scale dependent manner (Statzner & Higler 1986; LeRoy Poff 1996). Processes not only include the maintenance of species richness, but also the mechanisms that the animals use under these different circumstances, e.g., life history strategy. Rivers and streams can be considered as a habitat templates on which the animal's 'bauplane' adapts (Brusca & Brusca 1990; Southwood 1977). Associations between the disturbance frequency and habitat heterogeneity of a system and its fauna have been devised (Townsend 1989). In the general discussion (Chapter 7) the position of the three rivers examined are discussed in relation to this classification system.

1.4 Specifics of study

In an ecological context, the aims of this thesis were simple; to identify habitat patch preferences for benthic invertebrates and identify the relative importance of two scales, the larger being reach scale and the smaller at the scale of Surber (lambourn form) samples, thereby covering habitat produced by both meso and microform processes. The project concentrates on small rivers typical of those occurring in Scotland, from highland to lowland conditions: River Etive (Highlands), Blane Water (Central Belt) and the Duneaton Water (Borders): see Chapter 2 Section 2.2 for full site descriptions. All three river sites would be of middle order, 3-5. The river reaches studied here are all middle reaches and were expected to have a wide range of functional groups represented, in keeping with the River Continuum Concept. This study focuses on flow variables at what can be viewed as ambient, rather than disturbing, spatey discharges, and does not examine the impact of predators, disease or disturbance on the distribution of the macrobenthos.

There are a number of key mechanisms in ecology which could influence the identification of invertebrate habitat preferences and are addressed here before proceeding to the details of the study.

Firstly, a suitable model describing the state of the community has yet to be derived, making it difficult to decide whether the benthic invertebrate community was at equilibrium or in the process of recovering from disturbance in the rivers examined. Existing models such as the intermediate disturbance hypothesis do not successfully describe community structure (Malmquist & Otto 1987) although other workers (Death & Winterbourn 1995) support the theory of dynamic equilibrium at least at the patch level. So where possible, data on the long term flow variability of each site are provided. It was assumed that despite the constant redistribution of benthic invertebrates by flood events and invertebrate drift, optimal habitat patches will have higher numbers of animals due to 'bottlenecks' occurring in the more suitable habitats (Townsend 1980). It was therefore expected that the detection of habitat preferences of even very mobile benthic invertebrates was feasible.

The structure of this study and the choice of environmental variables focused on direct effects and therefore covers only a small subset of the potential interactions which can occur, e.g. those between the animals and their physical habitat, in the form of flow preferences it is unable to detect some of these interactions. The results presented should therefore be considered cautiously, especially as such key mechanisms as competitive exclusion may function causing some taxa not to be encountered in their preferred flow conditions if a more successful competitor has already monopolised them.

As mentioned earlier environmental conditions during the juvenile stage are highly important for the fecundity of these animals. Taxa which feed as adults were infrequently encountered in samples in this study, although some simulids and fully aquatic ceratopogonids were collected, both of which require blood feasts to reproduce in a maximal fashion (Williams & Feltmate 1994)[7]. In this study I have assumed that any correlations between physical variables and the distribution of benthic invertebrates reflects preferences of the juvenile stages and are not a function of adult habitat selection. This is valid given the lack of overhanging vegetation, which adults use as shelter, at all sites. Vegetation such as this has been reported to be influence juvenile distribution on the river bed indirectly as the vegetation attracts egg laying adults (Harrison, in press). Having now outlined the assumptions upon which the work is based I can proceed to the details of the study.

Crustacea, Insecta, Mollusca, Annelida and Platyhelminthes were all encountered in this study with both exopterygota and endopterygota insects represented. The hemimetabolic developers in this study are the Ephemeroptera and Plecoptera. The holometabolic taxa represented were the Trichoptera, Coleoptera and Diptera.

As mentioned earlier the rivers were chosen to represent the range of available conditions in the middle reaches of Scottish rivers. Excluding the similarities mentioned above the rivers differ not only in hydrology but a number of other factors. Like the majority of running waters found north of the Highland Boundary Fault, the River Etive is on resistant rocks, and consequently nutrient poor. The geology in the Borders and Central Valley (the location of the other sites used in this study) is mixed and the majority of streams would be naturally of intermediate nutrient level (McKirdy 1999; Werritty *et al.* 1994).

The steep gradients of many Scottish valleys can cause shading of the river bed reducing its productivity. The River Etive would be the most strongly effected of the three sites examined. Filamentous and encrusting algae are believed to be the main primary producers within the rivers examined in this study. The moss *Fontinalis* does occur in these rivers as does the macrophyte *Callitriche stagnalis,* but neither are known to be major sources of food for macrobenthos and were not found in the sections of river used in this thesis for the identification of general flow preferences (There is evidence that on occasion several common invertebrates will graze most soft macrophytes).

In Scotland, staining of water by humic acids from peat is common, giving the water a brown colour which reduces light penetration (Hutchinson 1957). Again the R. Etive is the site most likely to be affected by this phenomena, although the other two rivers have some peat in their upper catchments too. Underwater ice does occur in Scottish rivers and is likely to be common in the River Etive and Duneaton Water, both of which are at high altitude.

When choosing potential sites, frazil ice or possibly the first soft deposits of anchor ice were observed on the bed of the Upper Clyde at Abington, less than 20 miles from, and at the same altitude as, the Duneaton Water, one of the other sites examined in this study (see Hynes (1972) for ice definitions)[8]. The role of this natural form of disturbance is not known. It is clear however that there is a large amount of between site variation in

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[8] Trichoptera, Plecoptera and Ephemeroptera collected from the river bed ice remained immobile until they defrosted in the laboratory. Upon defrosting they became active and appeared healthy.

physical processes. At the very start of this chapter, I mention that studies often suffer from unclear definitions of the physical habitat. The first results chapter of this thesis tests the hypothesis that riffles and pools can be described visually in a consistent manner or with Jowett's rule (Jowett, 1993) which is based on ambient flow measurements, e.g., that these habitat units have constant physical characteristics at the three rivers examined and that the benthos exhibit preferences for these habitat units irrespective of all the other physical variables which may influence their distribution.

Recent work suggests that hydraulic habitat may be extremely important. Studies on a regulated river in Norway have shown that growth rates of *Baetis rhodani* increased post regulation by ten to twenty times, (Raddum & Fjellheim, 1993). It was suggested by the authors that, the reduced flow, subsequent increase in summer temperature and retention of organic matter contributed to the increased carrying capacity for this animal. The animal's life cycle was also one month faster. Increased discharge, on another regulated Norwegian river, appeared to cause an overall reduction in biomass of invertebrates (Fjellheim et al. 1993). At this site, rheophilic species increased in biomass, but lentic species' biomass decreased. These result suggests that indirect effects of altered flow parameters are important and can have both positive and negative, sub-lethal effects on benthic invertebrates. By identifying hydraulic habitat preferences of benthic invertebrates it was hoped that this work would improve approaches to habitat creation in river restoration and rehabilitation schemes. A potential mechanism underlying these observations is that the physical flow habitat is patchy and that invertebrates find some patches more suitable than others. Chapter three, the second results chapter, tests the hypothesis that benthic invertebrate distribution is patchy at the surber sample scale and dependent on flow variables. By using multivariate analysis I was able to test the amount of variation in the benthic invertebrate community structure explained by flow variables.

As mentioned earlier, Townsend (1980) has postulated that it is possible to detect benthic invertebrate patch preferences. By inference, if the animals are choosing patches on the basis of flow conditions we should be able to detect this by increased abundances in their preferred patches. Chapter 4 examines the responses of individual species to flow variables. There is a presumption that taxa will congregate in areas with suitable habitat conditions, frequently leading to the animal's abundance showing a unimodal response to environmental variables, Jongman *et al* (1988). I test the responses of individual taxa to see if they exhibit a unimodal response. This also allows us to visualise the degree of niche overlap along these environmental variables at the different sites. As sampling effort was not equal at all points along the environmental variables gradients –samples were taken randomly - it is possible that any positive responses are an artefact of the sampling regime. This aspect is also investigated.

Chapter five presents the results of flume experiments designed to detect the upper flow preferences of benthic invertebrates. The main aim here was to try and replicate the results of the field data.

The final results chapter addresses the use of an instream macrophyte species, *C. instagnalis* by invertebrates. In particular the diversity of flow conditions within the plant is examined and related to the distribution of invertebrates. The hypothesis tested is that different sections of the plants support different benthic invertebrate assemblages and that these are consistent between different plants at the same site. That the outside of the plants, where velocity is highest, supports a more limited fauna is explored.

1.5 Thesis outline

- *Chapter 2* is the first of three concentrating on the ecohydrology of three Scottish rivers. It focuses on large scale habitat units; riffles, runs and pools. General descriptions of the hydrological habitat of reaches examined are given. Jowett's rule for objectively identifying riffles, runs and pools is assessed and the biological implications discussed. The following two chapters focus on finer physical scales.
- *Chapter 3* discusses the distribution of benthic macroinvertebrates in relation to hydraulic environmental variables at a finer physical scale than the previous chapter. Ordination analysis is used to find patterns in the macro-invertebrate distributions; aggregations or associated clumps of taxa. The structure of the community is then related to the environmental variables measured, the relative importance of the variables is discussed.
- *Chapter 4* reports individual taxon response curves to the flow variables measured. The applicability of Gaussian response curves to such data is investigated as is the importance of availability of the environmental variable on the response of the taxa. Plasticity of species responses is discussed as are the implications of deriving habitat simulation models from such data.

- *Chapter 5* investigates the responses of individual benthic invertebrates to high velocities. Behavioural observations are presented and some data on morphometrics of *Ecdyonurus.*
- *Chapter 6* compares the abundance and diversity of benthic invertebrates within stands of *Callitriche stagnalis* to substrate without vegetation. The hypothesis that the outside of stands represents an extreme environment are examined by comparing the fauna of the outer part of stands to that found in the middle and underneath. Data on the evenness and abundance of taxa is presented. It is suggested that plant architecture and velocity combine to create a range of stability and thus microhabitats.
- *Chapter 7* contains a general synthesis of all the results and their implications for benthic macroinvertebrate ecology and discusses how each set of results complements one another.

Chapter 2: Hydraulic and invertebrate surveys of reaches in the Blane Water, River Etive and Duneaton Water

2.1 Introduction

Fundamental to river rehabilitation is the ability of researchers to describe a river reach in language understood by both engineers and ecologists. Engineers and geomorphologists are increasingly required to understand ecological requirements when designing flood alleviation schemes and other works. Although frequently working on a smaller physical scale, ecologists have increasingly recognised the potential of hydrological studies and techniques to describe the world of benthic invertebrates. In the next three chapters I follow this trend by examining the hydraulic world of invertebrates using a combination of ecological and engineering techniques.

Hydrological techniques have been applied to ecological studies in a rather piecemeal manner, which has tended to make comparison of the applicability of such techniques difficult. Hence in the recent ecological literature there have been calls for a consistent systematic approach to hydraulic surveys of invertebrate microhabitats (Davis & Barmuta 1989; Carling 1992). Davis lists a standard hierarchy of hydraulic parameters to use when surveying invertebrate habitat, which is used here in a modified form. The upper echelon of this hierarchy, involves measures of entire reaches, and it proceeds down the physical scale to measurements of flow around individual stones, transcending the scales used by engineers and ecologists. Results collected by using the entire hierarchy facilitate an interdisciplinary understanding and allow comparisons between work by different ecologists using the same methods.

The data presented in the next three chapters were collected over a survey period of two months using the hierarchical approach mentioned above. The chapters are structured on two themes. The first theme is physical and the second biological. This chapter compares the three rivers investigated at the reach scale. The next chapter uses data gathered on a smaller physical scale to compare community structure in relation to flow parameters at the three sites. The final chapter concentrates on the responses of individual taxa to flow, and possibilities for modelling these preferences. This layout of results has the benefit of making the transition from a larger physical scale familiar to engineers, to the finer scale important to invertebrates.

In this chapter I attempt to differentiate between riffles, runs and pools (20m reaches) using objective hydraulic data and individual taxon preferences. I also looked at the same question subjectively by seeing if invertebrates identified elsewhere as having preferences for either riffles or pools did so at our sites.

Riffles and pools are bed forms viewed by geomorphologists as possible primary determinants of meanders and as discrete habitat units by ecologists, with runs somewhat intermediate between the other two structures. In both disciplines an abiding problem is the reliable identification of these units. Investigators rarely give specific criteria. Where criteria are given they tend to be relative visual estimates. Riffles are frequently defined as steep, shallow reaches of fast, shallow flow with the water surface broken by emergent substrate. Pools are deep slow reaches with an unbroken surface, and runs are intermediate in form.

A number of techniques have been described which identify pools and riffles in a more objective manner. Jowett (1993) has categorised these into those based on: substrate size, water surface slope, the ranges of water depths and velocities, bed topography, Froude number and water surface characteristics. Which criteria one uses depend on the purpose of the survey: geomorphologists tend to use changes in bed topography and ecologists water depth to velocity ratios.

As objective measures, water surface slope and measures of longitudinal bed profiles are the best. The main advantage of using changes in longitudinal bed slope, from a geomorphologist's point of view is that it is independent of discharge (unless discharge is high enough to mobilise the bed). However this is the main disadvantage for ecologists who are interested in studying aquatic invertebrates, as a riffle chosen using this criterion may be dry when one goes to sample it, or its size may have altered significantly from when it is first identified. A combination of water surface slope and longitudinal changes in bed topography which can be assessed at the same time of sampling, is most practical.

In this chapter I describe the survey reaches I studied using some of these criteria. Following Jowett (1993) I also attempt to determine which physical parameters best differentiate between riffles and pools.

As mentioned earlier, riffles and pools are viewed as distinguishable habitat units by ecologists. This is most clearly evident in their use by fish, particularly by salmonids. Invertebrate communities have been shown to differ between riffles and pools, with riffles exhibiting greater species richness (Briggs 1948; Brown & Brussock 1991; Egglishaw & Mackay 1966; Surber 1937; Wohl *et al.* 1995). Species composition differs between riffles and pools reflecting the functional groups of the species present. Higher numbers of collector gatherers, shredders and predators tend to be found in pools (depositional areas). In riffles (erosional) these groups and filterers tend to be represented too (Wohl *et al.* 1995) (NB Wohl does not include scrapers in his assessment). The ability of heterogeneous habitats (riffle) to support greater species richness is dealt with elsewhere but the capacity of riffles to support a more diverse range of functional groups than pools may be part of the explanation for this phenomena. Care must be taken in interpreting these examples as contrary findings do exist.

Armitage (1976) reported that on the River Tees, species richness is not highest in riffles but is highest in the pools. This river was organically enriched which may have lead to the high numbers of Mollusca, Hydra and *Nias* sp. which the author attributes to the high diversity in Tees pools. The velocities encountered in Tees riffles were notably high, 0.5-0.75 ms^{-1} which may explain why they did not have the highest diversity of invertebrates.

Biomass of invertebrates, (Wohl *et al.* 1993) a factor not addressed in this thesis, can be greatest in either riffles (Briggs 1948; Brown & Brussock 1991; Surber 1937) or other less heterogeneous areas including pools (Armitage 1976; Egglishaw & Mackay 1966; Hynes *et al.* 1976).

A suite of other factors interact with the depth velocities typical of riffles and pools to make these habitats selectively attractive to certain groups. As pointed out by Brown (1987) adult riffle beetles (Elmidae) probably require water highly saturated with oxygen for their breathing apparatus to function; they use an air bubble as a plastron which absorbs oxygen from the water as it is used up the animal in respiration by diffusion. The need for highly saturated oxygen conditions is also thought to be important in the distribution of Plecoptera and Ephemeroptera and has been suggested as a possible reason for their perceived preference for riffles (Nagell & Larshammar 1981).In the study described here I examine the distribution of laminar flow between riffles and pools. Laminar flow conditions, which have the potential to limit oxygen diffusion in rivers can occur in two different flow structures. Firstly the entire boundary layer can be laminar or alternatively laminar sublayers to a turbulent boundary layer are formed near the river bed. Whether laminar flow occurs is dependent on the velocity of the river and bed roughness. If water flow is laminar, diffusion of dissolved gases and excreta is limited to a molecular rate, potentially leading to toxic build up or (hypo) anoxia in the vicinity of an animal. In turbulent water the random motion of molecules increases the diffusion rates preventing such adverse conditions (Moog & Jirka 1999). Some caddis can use their cases to increase flow rates over their gills and this could potentially provide a mechanism for dealing with laminar flows (Williams *et al.* 1987). Under a fully developed turbulent boundary layer a laminar sublayer may be present. Previously it has been suggested that this may provide a refuge from turbulent flow for benthic invertebrates (Ambuhl 1959). This theory was based on flume studies which over - estimated the depth of the sublayer and was refuted by work using more accurate flow measurement devices; laser doppler anometry (Statzner & Holm 1982) However this study was also based on flume work and to date no field results on the existence or otherwise of the laminar sublayer at invertebrate sampling points have been published.

This chapter has a number of aims which if condensed into one, would be the clear description of hydraulic habitat at the three rivers examined at a riffle-pool scale and the determination of any evidence that invertebrates distinguish between these habitat units. Specifically the first aim is to test Jowett's rule for differentiating between pools, riffles and runs and comparing the results of it to visual categorisation, (Jowett 1993). This rule uses cut of values of dimensionless combinations of flow variables, e.g. Froudes number and a velocity-depth ratio. I attempt to see if the same cut of points work at my sites.

The second aim is to test the hypothesis that invertebrate community composition is not statistically different in the deep and shallow examined.

The final aim is to report estimates of near bed flow conditions and by so doing show that, in the field laminar sublayers to the boundary layer are rare. The chapter also contains a general description of the river sites examined.

2.2 Methods

2.2.1 Site choice

In an effort to cover the range of stream types found in Scotland a lowland river, an upland river (rithron in nature) and a river in agricultural land with a flow regime intermediate in character between the other two rivers, were sought for the study. A number of potential rivers were screened using the following criteria:

- Non-channelled reaches of river were available with sample reaches devoid of macrophytes. (The effect of macrophytes on flow and therefore indirectly on invertebrate distribution is covered in a later chapter.)
- High Water Quality - Scottish Environment Protection Agency (SEPA) biological and chemical water quality monitoring showed the rivers selected had high water quality and a diverse invertebrate community. Where possible SEPA could also provide long-term flow data.
- Accessibility - Each site was within 2-3 hours drive of Glasgow. All sites were accessible by road and riparian owners were willing to allow sampling.
- Presence of pools and riffles - Suitable reaches were present which could be visually categorised as riffles or pools.

Prior to the commencement sampling a number of rivers in each category were assessed in this manner. Candidate sites were chosen and searched for suitable reaches. Where reaches did suit qualitative samples of invertebrates were taken and identified to genus. Candidate intermediate rivers included the Mouse Water, North Medwin, the Upper Clyde, Douglas Water and Duneaton Water; candidate lowland rivers included the River Endrick, Douglas Water (flowing into Loch Lomond), River Kelvin (upper reaches), Bannock Burn and the Blane Water; candidate highland rivers included River Etive and rivers flowing of Rannoch Moor and those flowing into Loch Rannoch. The three rivers selected best met the criteria outlined above: these were the Blane Water, River Etive and the Duneaton Water, see Fig 2-1.

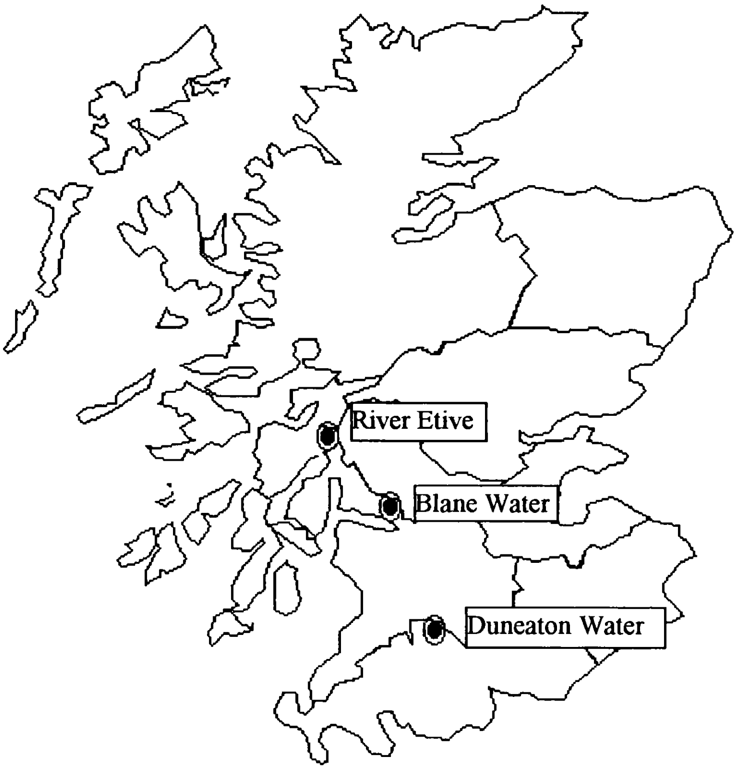


Figure 2-1 Map of Scotland showing the locations of the 3 rivers sampled.

2.2.2 *Description of sites*

The chosen rivers fall into three of the four categories defined by the UK River Habitat Survey (RHS): Steep streams (River Etive), Mountain valley rivers (Duneaton Water) and Small lowland rivers (Blane Water). The fourth category (chalk streams) is non-existent in Scotland and hence the survey was representative of major Scottish river types, although limited to three sites.

The River Etive (NN 224 521 UK National Grid Reference) is an upland stream located north of the Highland Boundary Fault. Its upper catchment is largely occupied by Rannoch Moor, a blanket peat bog overlying igneous resistant rock. Many feeder streams are acidic but the main channel is circumneutral (pH 6.96, spot measure). The catchment is generally unproductive with a low specific conductivity (mean conductivity 62 μS cm^{-1}). The site was sampled between the 9 and 30 August 1996. The river forms the southern border of the Glencoe Regional Park. SEPA figures available for the river downstream of the sampling point at site NN 136462 show average annual rainfall at 2.5 l per annum, and average daily flow as 9.671 m^{3}s^{-1}. The river's invertebrates have previously been studied as part of the extensive and excellent survey of highland streams (n = 52) by the Freshwater Fisheries Laboratory at Pitlochry in the 1960s (Morgan & Egglishaw 1966), at a site upstream of the study area used here.

The Duneaton Water (NS 869 221) is located at the head of the R. Clyde catchment and is a major tributary of that system. Geology in the catchment is mixed and includes coal seams and a range of other marine sedimentary rock types . Land use is mainly mixed farming with heathland in the upper catchment. A SEPA gauging station downstream from the site recorded minimum flow as 0.356 m^{3}s^{-1} and maximum flow as 85.390 m^{3}s^{-1} between 1993 and 1996. Standard annual rainfall was 1.33 l. The site was sampled between the 17-19 July 1996.

The Blane Water (NS 507 852) is a tributary of the R. Endrick and lies some 25 km north of Glasgow. The site is situated in an agricultural area, downstream from a trout fishery, and the river is quite nutrient rich. Lower Red Sandstone dominates the geology at the site and within the catchment with a small pocket of Upper Red Sandstone north of the site at Killearn and calciferous sandstone and basaltic lavas present in the top of the catchment. Glacial clay covers the bedrock throughout. A full discussion of the biology and geology of the Blane Water is given in Doughty & Maitland (1994). The site was sampled between the 3 and 9 July 1996.

2.2.3 *Field measurements*

Two reaches were chosen at each site, one deep and one shallow, estimated visually to be riffles and pools. Riffle reaches had steeper bed gradients than the adjacent pool reach and the water surface was broken. At the Etive site a clear riffle-pool sequence did not exist. The 'riffle' reach did however have a steeper bed gradient and was shallower than the pool with a lower mean velocity; see Table 2-1.

Table 2-1, Channel characteristics at the station reaches.

	Reach	Mean depth (cm)	Width (m)	Mean velocity (ms^{-1})	Mean slope
Etive	A deep	37.0	23.9	0.096	0
	B shallow	15.7	24.6	0.291	0.01232
Duneaton	A deep	22.1	9.0	0.072	0.00022
	B shallow	13.7	3.7	0.271	0.00567
Blane	A deep	22.1	15.3	0.182	0.00455
	B shallow	7.6	8.1	0.350	0.01695

A hydrological survey of each reach (station) was undertaken to quantify available habitat. The method used was a version of Instream Flow Incremental Methodology (IFIM) previously adapted successfully for estimating available invertebrate hydraulic habitat (Jowett *et al.* 1991). At each reach flow measurements were taken across a total of 10 transects, at 1m intervals, 0.5 m from the banks, and at the banks (only eight transects were sampled in each reach at the Blane Water; this was due to the flow meter breaking down). Transects were marked out in a sequential manner, at 1 m intervals, moving upstream. The flow measurements included mean water column velocity (mwc) and depth, which were measured using a SENSA electromagnetic velocity meter on a calibrated rod.

At three random sampling points, across each transect, invertebrate density and additional flow variables were sampled. Flow variables included, substrate composition and a velocity profile. Substrate type was visually estimated (% scale) using the following particle size scale: sand (0.06-2 mm nominal diameter), fine gravel (2-10 mm), gravel (10-64 mm), cobble (64-256 mm), boulder (>256 mm) and bedrock (solid rock surface) (Jowett *et al.* 1991). A velocity profile of 10 points was also recorded. It was not always possible to record velocity profiles as the water was too shallow or no flow could be detected and water depth sampled was limited to 1.5 m.

Quantitative benthic invertebrate samples were taken using a Lambourn sampler (frame size 1375 cm^2) at 3 random points across each transect. The Lambourn sampler had a heavy skirt attached around its base to prevent loss of animals. Invertebrate samples were preserved immediately in 70% alcohol. An equal amount of effort was expended on collecting each invertebrate sample. Large substrate particles were scrubbed using a nailbrush, after which remaining substrate was disturbed for 2 minutes to a depth of 10cm. All samples were sorted on white trays and animals identified to the following taxonomic levels: Annelida to subclass; Diptera to family, genus and species; all other taxa to genus or species. As identification to species was not possible in all cases animals were assigned to operational taxonomic units (OTU).

2.2.4 Estimation of hydraulic parameters from velocity profiles

Hydraulic parameters were calculated to give a hydrological description of the two reaches. Froude and Reynolds number were calculated from depth and mean water column velocity at each sampling point. Shear stress, shear velocity and Reynolds roughness number were derived from lognormal plots of velocity profiles, see Appendix II for an example and below for definitions of parameters. These parameters are thought to be useful descriptors of near bed flow for ecologists (Davis & Barmuta 1989; Young 1993). Davis & Barmuta (1989) was used as the source for the correct equations and choice of parameters. More recent clarifications of definitions and applications of some of these equations exist and were applied when necessary (Carling 1992; Young 1992) (Carling 1993; Lamouroux 1993). Appendix II assesses the limitations of the technique.

Only parameter estimates generated from profiles which were statistically significant ($P \leq 0.05$) were used, see Appendix III. This was based on the premise that being dependent on the log normal relationship the parameter estimates are only valid when the relationship is shown to exist, e.g., where it is statistically significant (Dingman 1984, Carling 1992, Smith 1975). Where data taken close to the substrate produced a lognormal profile, disturbed only by gross turbulence higher up in the water column, a truncated version of the profile was used; that is the lognormal readings were used on their own. Recent evidence suggests this may give better estimates of shear stress in the field (Biron *et al.* 1998). The data from non-significant profiles was not completely discarded. In chapter 3 (Section 3.2.1) mean water column velocity was generated from the profiles and used in the multivariate ordinations, e.g. these points were included in the 'larger dataset'.

Classification of Flow

Reynolds numbers were calculated for each point of each reach. Re is given by:

$Re = (UxD)/v$

Where U = mean velocity, D = depth and ν= kinematic viscosity. Reynolds number describes whether mean flow is laminar or turbulent. Froude number further differentiates flow. Froude number is given by:

$$Fr = U / \sqrt{gD}$$

Where g = acceleration due to gravity $9.8m^2s^{-1}$. When Fr < 1 flow is designated sub-critical (tranquil).

Flow in rivers usually forms a fully developed boundary layer. When this is the case a velocity profile measured up through the water column can be used to measure hydraulic parameters (see Appendix II). When the velocity profile is plotted on a lognormal graph, shear velocity (u*) and equivalent bed hydraulic roughness (k_s) can be calculated. Shear velocity is inversely proportional to the gradient of the velocity profile and z_0 (characteristic roughness length) can be calculated by extrapolating the regression line to zero velocity. The variable z_0 can be taken as an estimate of k_s.

These variables are useful in classifying near bed flow. Reynolds roughness number (Re_*) can be calculated from these two variables.

$$\mathrm{Re}_* = u_* k_s / v$$

Critical values of Re_* delineate flow as to the presence of the laminar sublayer of the boundary layer. Where the laminar sublayer is present its thickness (δ) can be estimated as follows:

$$\delta = 11.6 v / u_*$$

2.2.5 Statistical Analysis

Mann Whitney U tests were used to examine differences in Reynolds number, mean water column velocity and, depth measurements between deep and shallow reaches

(Sidney, 1956). Spearman rank correlations were performed on the variables to identify relationships between them. Discriminant Analysis was used to select the variable which best distinguished between the deep and slow reaches. Discriminant analysis is a parametric test which requires the data to be normally distributed. Square-root transformations were used to normalise data.

TWINSPAN was used to objectively separate deep and shallow reach invertebrate assemblages in each river. Twinspan (Two Way Indicator Species Analysis, (Jongman *et al* 1988) is a hierarchical divisive clustering technique which classifies sites and species by constructing an ordered two-way table from the site by species matrix. A CA axis is generated and then divided at its centre of gravity (centroid) (Jongman *et al* 1988). The two groups are then divided further. This dichotomous branching continues until a pre-set number of cuts have been under taken. Eigenvalues are quoted for each division and can be interpreted as P values.

TWINSPAN was chosen over the rival clustering techniques, because it not only provides a cluster analysis but also presents results in a table arrangement, which was particularly useful in this analysis. It is viewed as the best method for table arrangement and is recommended for hierarchical classification too (Gauch 1982). Gauch (1982) does not address the use of fuzzy-clustering which is useful with datasets where variation is continuous and TWINSPAN would force hard partitions on what is effectively non-discrete data (Equihua 1990). It works by allowing samples to belong to more than one group. This technique has been successfully applied to terrestrial invertebrate data (McCracken 1994). However the whole premise of this chapter is that there is a clear difference between the invertebrate populations in the deep and shallow sections of the rivers, a sample can only be in one or the other, not in both. Therefore TWINSPAN remained as the preferred ordination method.

2.3 Results

2.3.1 General Conditions

As expected, the deep reaches were slow-flowing and the shallow reaches faster-flowing, see Table 2-1. In the Blane water velocity (0.182 ms^{-1}) was quite high in the deep reach, being greater than half the velocity in the shallow reach (0.35 ms^{-1}). At the other two sites mean velocity in the deep reaches was a third of that in the shallow. This is in agreement with SEPA data which shows the Endrick/Blane catchment at the time of sampling (1.3 m^3s^{-1}) was below mean discharge (2.3 m^3s^{-1} averaged over 1993-98) for the sampling month, but that it had experienced an increase in discharge during the first sampling days, see Figure 2-2. That is it was experiencing a small summer spate. The Duneaton Water was below mean discharge (mean = 1.1 m^3s^{-1} averaged over 1993-98) for the sampling month (July) at the time of sampling, 0.5 m^3s^{-1}, see Figure 2-3. No long-term flow data on the Etive were available.

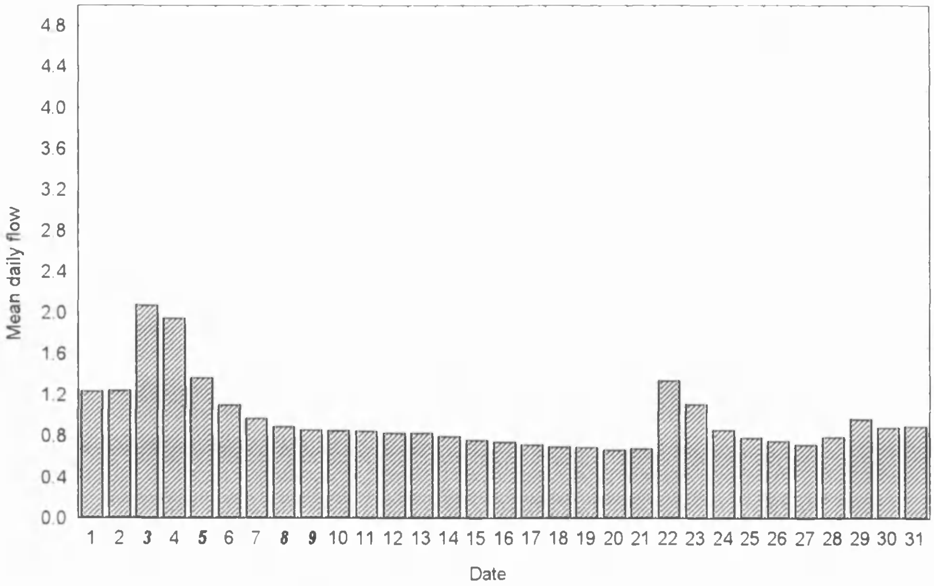


Figure 2-2 Mean daily flow in m^3s^{-1} (9am-9am) for the R. Endrick, of which the Blane is a tributary, July 1996. Data from the gauging station at Gaidrew (NS 485 866) courtesy of the Scottish Environment Protection Agency (SEPA). Sampling dates are in bold italic type.

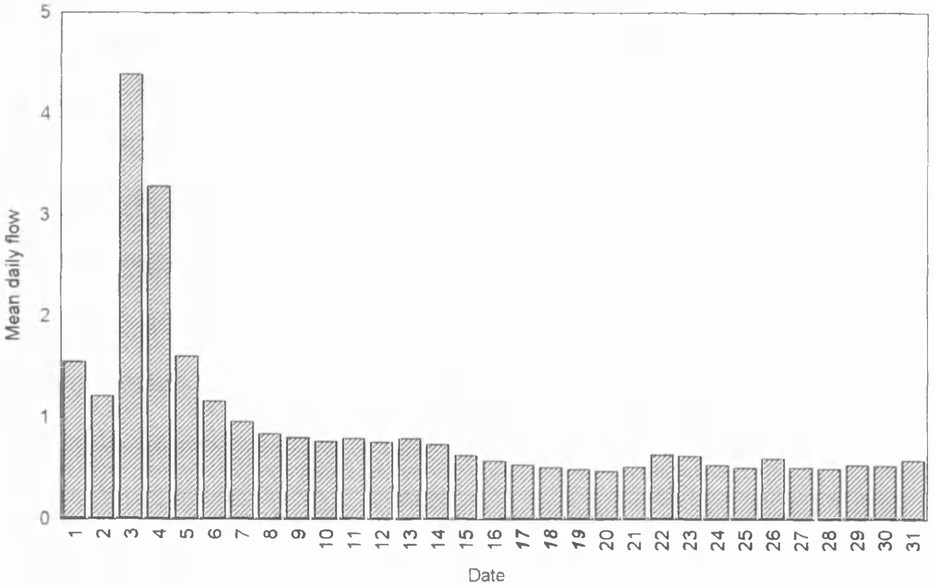


Figure 2-3 Mean daily flow in m^3s^{-1} (9am-9am) for Duneaton Water July 1996. Data from the gauging station at Maidencots (NS 929 259) courtesy of the Scottish Environment Protection Agency (SEPA). Sampling dates are in bold italic type.

As it was suggested that rivers like the R. Etive do not break down into a proper riffle and pool sequence (Fozzard, *et al* 1994) it is important to demonstrate whether the two reaches examined were in fact different. Median channel depth was significantly deeper in the pool than in the riffle area of the river (Mann Whitney U test W= 80152.0, P>0.0001 adjusted for ties, Pool N=261 Median = 31 cm Riffle N=233 Median = 15 cm).

2.3.2 Comparison of flow conditions at different sites

I wished to see if the magnitude of Reynolds number could be used objectively to show a difference between the riffles and pools chosen. In the case of the Blane and Duneaton Water, Reynolds number was significantly lower in the pools; Mann Whitney U test (Blane P<0.005 W=7938, Riffle N= 86 Median =37900, Pool N= 79 Median=20680), (Duneaton Water W=9224.5 P<0.0001, Riffle N=65 Median = 37620, Pool N=117 Median = 4200). There was no significant difference in Reynolds number between reaches examined in the Etive.

Previous studies have shown strong intercorrelations between the environmental variables which I used in this work. Some in fact are combinations of each other (Reynolds number and Froude number are both derived from velocity and depth measurements). A sub-set of measurements (those where substrate was also measured) were examined using Spearman Rank correlation; see Table 2-2. The same general trends show across all sites although there are site-specific differences. At all sites velocity was significantly and positively correlated with Froude and Reynolds numbers.

Table 2-1, Spearman rank correlation matrix of hydraulic variables. Values are combined from the deep and shallow reaches at each river. *P<0.05.

	velocity (mwc)	depth	substrate	Fr
River Etive				
depth	-0.07			
substrate	0.31*	-0.11*		
Fr	0.95*	-0.36*	0.33*	
Re	0.76*	0.56*	0.18*	0.53*

Duneaton Water				
depth	0.11			
substrate	0.6*	-0.02		
Fr	0.95*	-0.2	0.59*	
Re	0.88*	0.54*	0.51*	0.68*
Blane Water				
depth	0.23			
substrate	0.07	-0.003		
Fr	0.76*	-0.22	0.10	
Re	0.78*	0.75*	0.08	0.34*

Table 2-2 Classification success of discriminant models using velocity, depth, substrate, and Froude number. Analysis was performed on square-root transformed data from each river separately and then combined. All figures are percentage of correctly classified samples. N = 60 (Duneaton water , R. Etive), N = 48 Blane Water.

	deep A	shallow B	Total	P
River Etive				
Velocity	85	76	80	<0.00001
Depth	59	80	70	<0.001
Substrate	51	66	59	<0.05
Fr	88	80	84	<0.00001
Duneaton Water				
Velocity	68	75	71	<0.001
Depth	64	67	66	<0.01
Substrate	84	67	75	<0.00001
Fr	80	85	83	<0.00001
Blane Water				
Depth	73	68	71	<0.01
Fr	78	78	78	<0.01
Combined				
Velocity	69	72	70	<0.00001
Depth	54	72	64	<0.00001
Substrate	72	62	67	<0.0001
Fr	71	70	70	<0.00001

Depth also showed the same relationship with Reynolds number across all sites. Depth only showed a significant and negative relationship with Froude number in the Etive. Velocity showed a significantly positive relationship with average substrate size in the Duneaton and Blane. Depth was negatively correlated with substrate at all sites but only significantly so for the River Etive. Froude and Reynolds numbers were significantly correlated with all other variables. Froude number and depth at the Duneaton Water and depth and substrate at the Blane were exceptions, not being significantly correlated with either Reynolds number or Froude number. Discriminant analysis showed that all variables, with the exception of Reynolds number (it was not significant), could correctly classify riffle and pool reaches. In this subset of the data velocity and substrate showed no difference between riffle and pool reaches. This was not the case with the larger data set, where Reynolds number and velocity were different at these sites. Froude number consistently showed the highest percentages when it came to differentiating between the riffles and pools (always >70%: see Table 2-2). A combined model using all variables other than Reynolds number could identify higher percentages than any individual variable for the combined data set (77%). However it was believed that this result could be misleading (due to the high inter-correlations between variables) and the model was discarded.

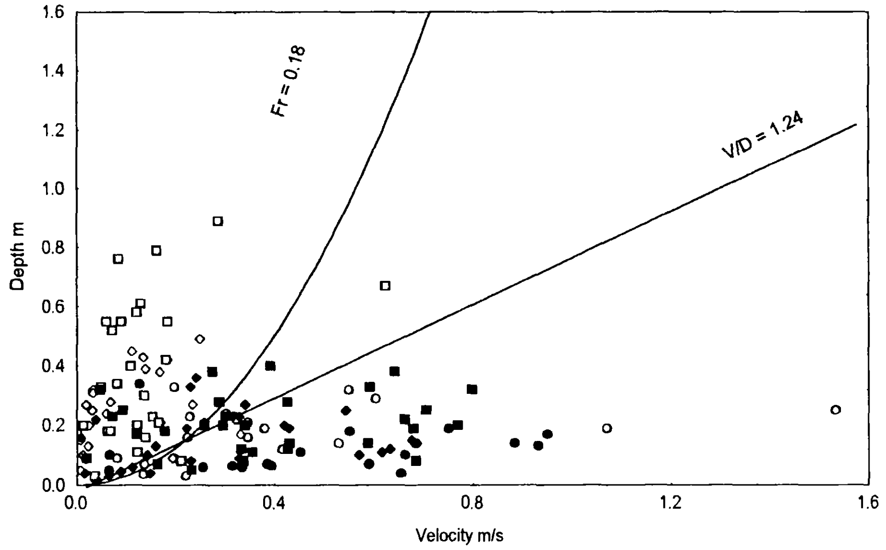


Figure 2-4. Classification of pool, run and riffle by velocity/depth (V/D) ratios of 1.24 and Froude number (Fr) of 0.18; using Jowett's rule any point with Fr less than 0.18 or V/D less than 1.24 is classified as a pool. Plot showing the combined deep (open) and shallow (solid) points for the three rivers from the smaller dataset (in which substrate variables were also measured); R.Etive (squares), Duneaton Water (diamonds), and the Blane Water (circles). For points with Fr > 0.18 and V/D > 1.24 (those not from pools) those from reaches with a surface slope of less than or equal to 0.0099 are classified as runs and as riffles if the slope was > 0.0099.

I applied Jowett's rule for differentiating between riffles, pools and runs, see Figure 2-4 and Table 2-3. Based on the outcome the deep and the shallow reaches have been assigned to the distinct categories, see Table 2-3. As can be seen from Figure 2-4 not all sampling points from one reach were in the same category, so I allocated one of the categories to each reach on the basis of which category predominated for the reach e.g. which category had the greatest number of points.

Table 2-3 Categories reaches sampled were allocated to using Jowett's rule

River	deep	shallow
River Etive	Pool	Riffle
Duneaton Water	Pool	Run
Blane Water	Run	Riffle

2.3.3 *Substrate available in the reaches*

Substrate type at the three sites reflected their ambient flow conditions. The R. Etive was dominated by boulder, cobble and gravel (Figures 2-5, 2-8). The Duneaton Water was intermediate between the other two rivers having a high proportion of cobble in the faster reaches, but generally being dominated by gravel and sand (Figures 2-6, 2-9). The Blane water had hardly any large substrate elements and was almost exclusively dominated by gravel (Figures 2-7, 2-10). With the exception of the Blane, in the shallow reaches, larger substrate elements were more dominant than in the deep reaches. To a small extent, the mixture of available substrates was greatest in the deep reaches.

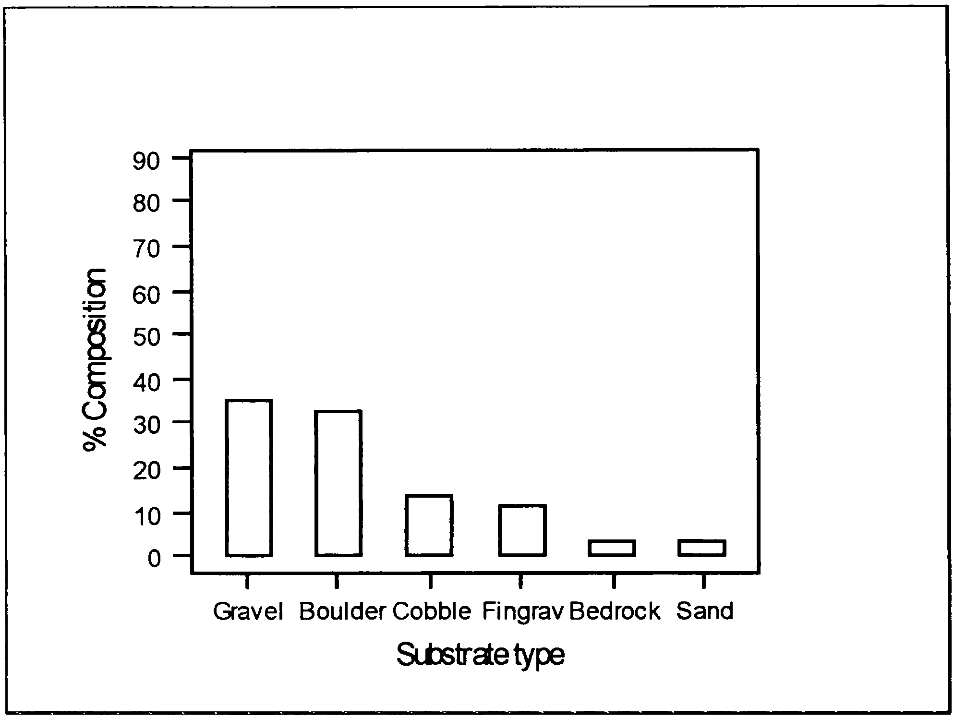


Figure 2-5, River Etive: substrate composition of the deep reach (a). Fingrav = Fine gravel

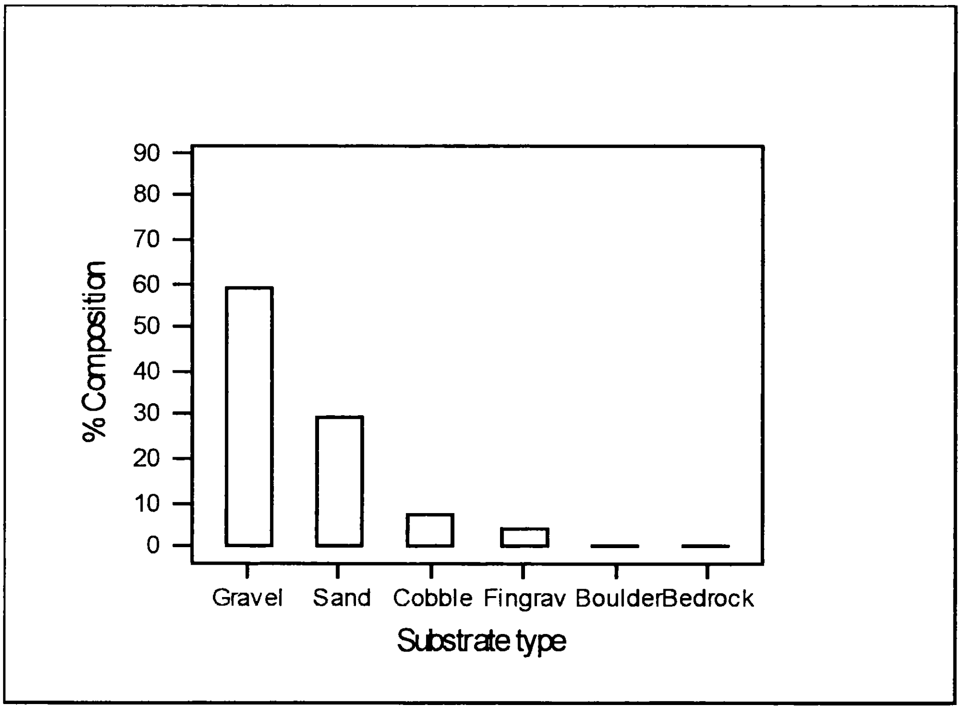


Figure 2-6, Duneaton Water: substrate composition of the deep reach (a).

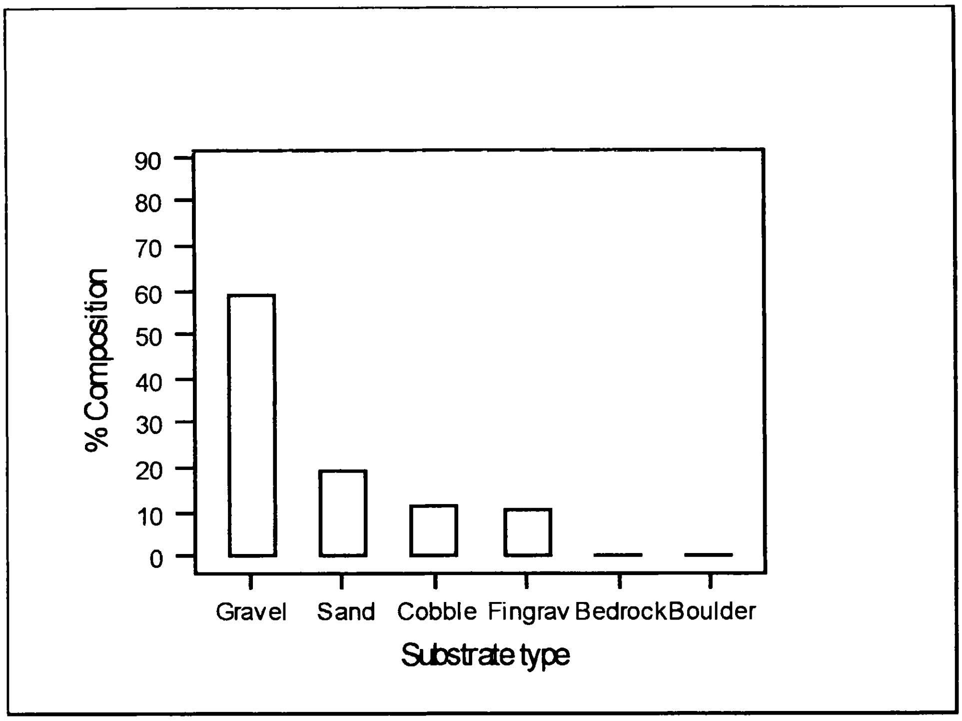


Figure 2-7, Blane Water: substrate composition of the deep reach (a).

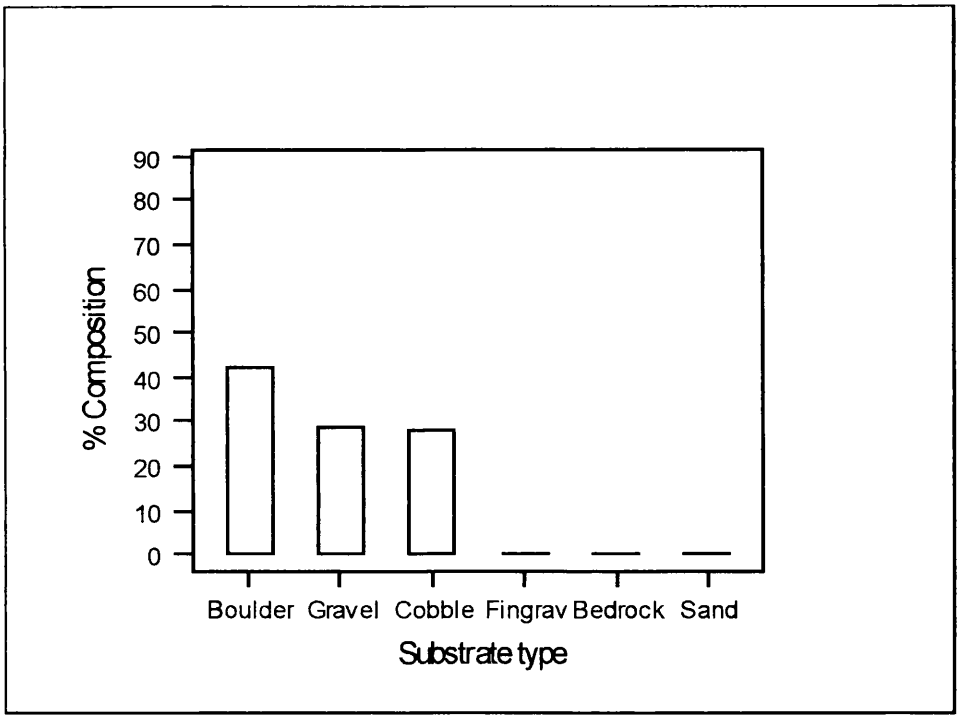


Figure 2-8, River Etive: substrate composition of the shallow reach (b).

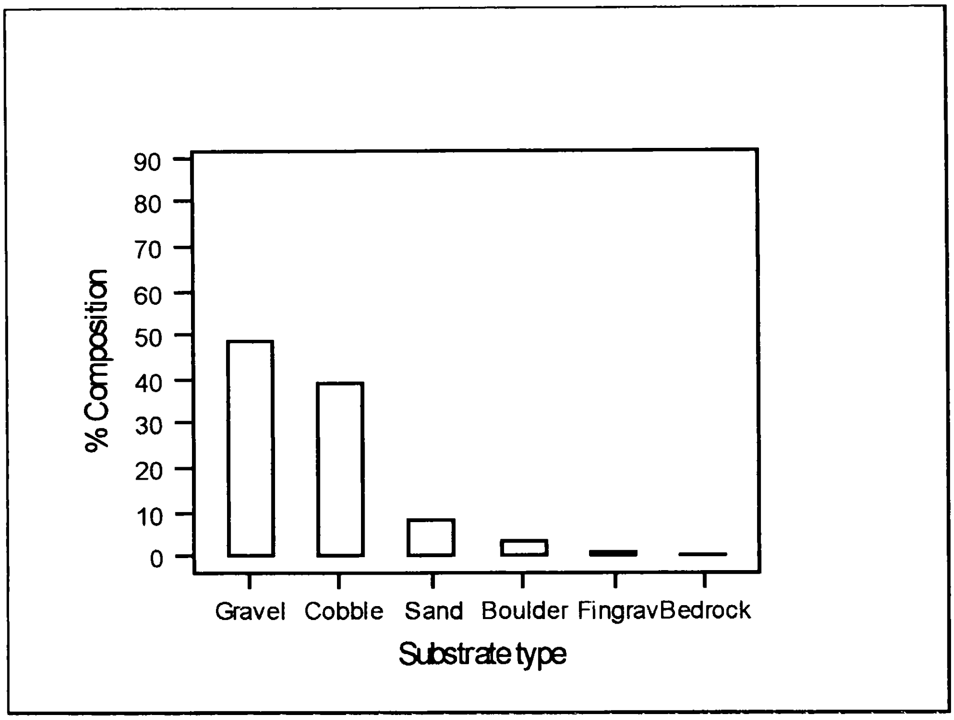


Figure 2-9, Duneaton Water: substrate composition of the shallow reach (b).

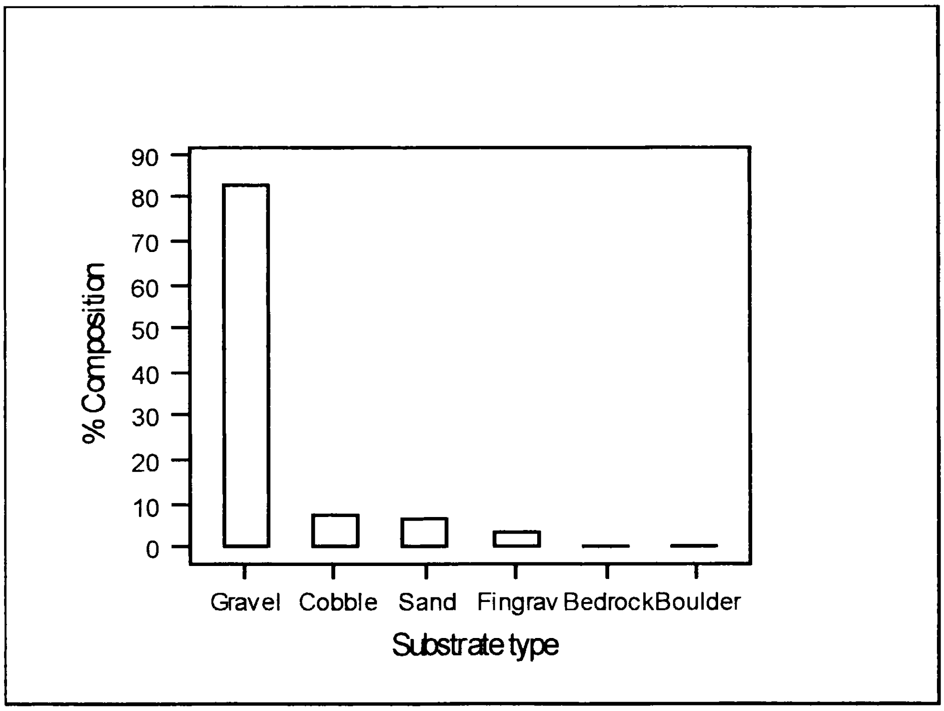


Figure 2-10, Blane Water: substrate composition of the shallow reach (b).

Only two thirds of the 136 velocity profiles recorded at the three rivers could be measured with sufficient accuracy to estimate the presence and depth of the laminar sub-layer. In cases where it was impossible to measure velocity profiles accurately this was due to the gross turbulence of the water and it is reasonable to assume that a laminar sub-layer would be prevented from forming in such conditions. Laminar sub-layers were rarely present elsewhere and when present were <1mm thick (Table 2-4).

Table 2-4, Characteristics of the laminar sub-layer of the boundary layer.

SITE	N	Depth of Laminar sublayer	Smooth Present	Transitional Disrupted	Rough Absent
Etive	27	0.4 mm	8	12	15
Duneaton	34	0.9 mm	8	20	9
Blane	36	1 mm	3	11	17

2.3.4 Distribution of Turbulent and Laminar flow within reaches

Water flow at all sites was predominately turbulent or transitional, see Figures 2-11 to 2-13. Where flow was laminar it was in shallow water, near the channel margins. Flow was also predominately sub-critical (tranquil) as determined from critical values of Froude number.

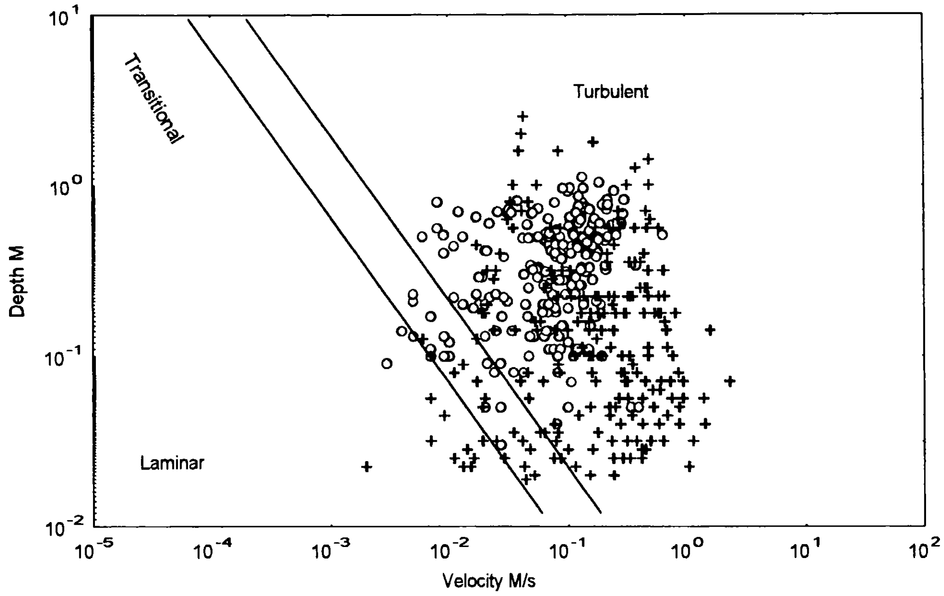


Figure 2-11. Variation in turbulent flow in the River Etive. O denote the shallow reach and + denote the deep reach. The parallel lines demarcate the area of transitional flow Re = 500-2000 (Smith 1975).

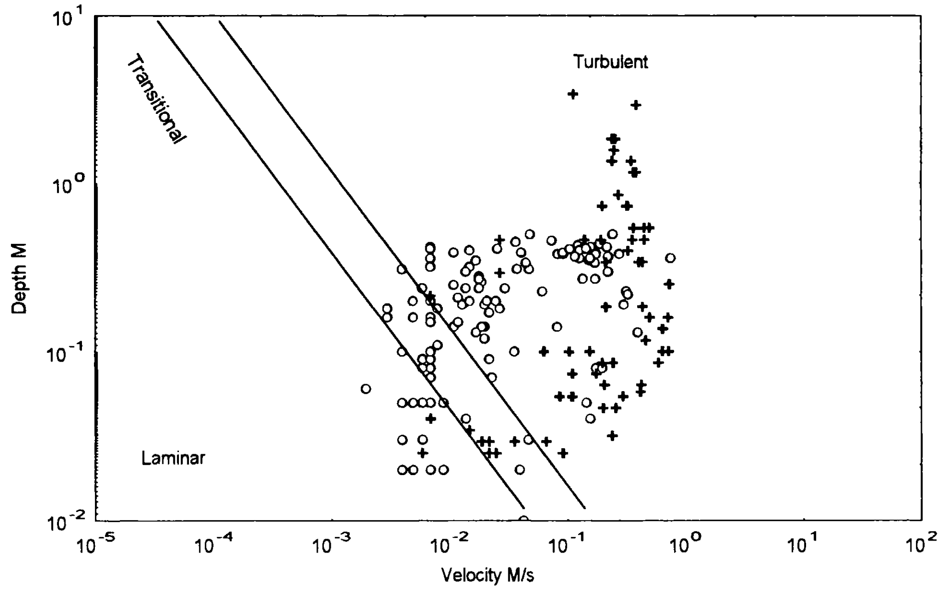


Figure 2-12. Variation in turbulent flow in the Duneaton Water. O denote the shallow reach and + denote the deep reach. The parallel lines demarcate the area of transitional flow Re = 500-2000 (Smith 1975).

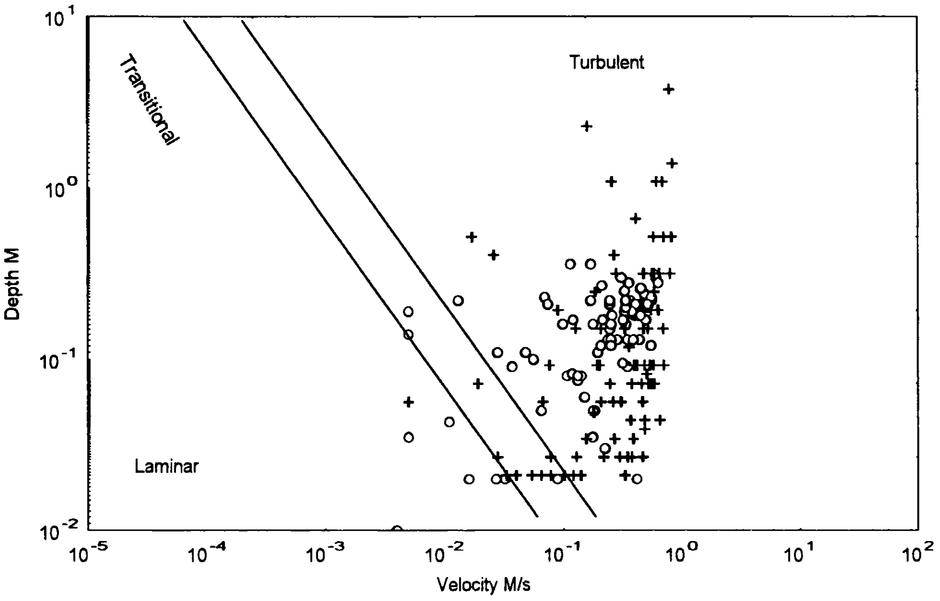


Figure 2-13. Variation in turbulent flow in the Blane Water. O denote the shallow reach and + denote the deep reach. The parallel lines demarcate the area of transitional flow Re = 500-2000 (Smith 1975).

2.3.5 Species lists

A comparison between the species composition of the reaches was performed on a river by river basis. Table 2-6 gives the taxa list for all sites. A comparison of the invertebrate assemblages in the deep and shallow reach of each river was performed using TWINSPAN analysis, but it did not separate them clearly; data shown in Appendix IV. At both the Blane and the Duneaton Water either the Chironomidae or Ephemeroptera were numerically dominant. In the R. Etive, Trichoptera (mainly *Hydroptila sp.*) were the most dominant with Ephmeroptera and Chironomidae the next most dominant groups.

Table 2-5. List of taxa present in the deep (A) and shallow (B) reaches of the three rivers. Some taxa were identified to different levels depending on the quality of specimens. Chironomidae from the R. Etive were identified to genus and are presented in a second table. Names standardised to those in (Maitland 1977).

Operational Taxonomic Units	OTU code	Etive		Blane		Duneaton	
		A	B	A	B	A	B
Oligochaeta	Olig	48	10			26	22
Lumbricidae	Lum					2	1
Hirudinea	Hir					8	4
Succinea	Suc					3	1
Ancylus fluviatilis Muller	Anfl			14	40	12	5
Potamopyrgus jenkinsi (Smith)	Poje			1	1		
Hydracarina	Hydra					7	1
Gammarus pulex (L.)	Gapu			19	72	3	4
Asellus aquaticus (L.)	Asaq			6	18		
Limnius volckmari (Panzer)	Livo	23	29	41	71	8	45
Oulimnius	Ouli	0	2	35	48		
Oulimnius tuberculatus	Outu					27	8
Oulimnius troglodytes	Outr					0	1
Esolus parallelepipedus	Espa					5	3
Elmis aenea (Muller)	Elan			19	44		
Dytiscidae	Dyti	2	0				
Dytiscidae Oreodytes?	Dyor			5	1		
Chironomidae	Chir			>1000	>1000	527	129
Tanypodinae	Tany	10	9				
Orthocladiinae	Ortho	13	31				
Diamesinae	Dia	0	2				
Simuliidae	Simu	0	3			0	75
Tipulidae	Tipu	13	6			53	100
Baetis rhodani (Pictet)	Barh	12	24	4	43	8	64
Baetis scambus Eaton *group*	Basc					3	9
Caenis rivulorum Eaton	Cari	1	14				
C. luctuosa (Burmeister)	Calu	0	1				
Ephemerella ignita (Poda)	Epig	23	16	526	597	107	185
Ecdyonurus Eaton	Ecdy	0	2	67	75	86	265
Rhithrogena semicolorata	Rise	1	4				
Heptagenia Walsh	Hept	2	7				
Ephemera danica Muller	Epda			0	1		
Siphlonurus armatus Eaton *?*	Siar	0	1				
Leuctridae Genus?	Lege			77	99	3	5
Leuctra moselyi Morton	Lemo	3	2			28	92
Leuctra fusca (L.)	Lefu					2	49
Perlodes microcephala (Pictet*)*	Pemi	0	2			0	1
Perla bipunctata Pictet	Pebi	0	1				

Operational Taxonomic Units	OTU code	Etive		Blane		Duneaton	
		A	B	A	B	A	B
Hydroptila sp. Dalman	Hydr	86	21				
Oxyethira sp.	Oxyt	16	1				
Polycentropus kingi McLachlan	Poki	3	4				
Polycentropus flavomaculatus	Pofl	8	5	1	0		
Plectrocnemia conspersa	Plco	1	3				
Rhyacophila septentrionis	Rhse	1	2				
Rhyacophila dorsalis (Curtis)	Rhdo			1	3	0	3
Agraylea multipunctata Curtis	Agmu					0	1
Hydropsyche sp.	Hydro					0	10
Hydropsyche siltalai	Hysi			3	6		
Rhyacophilidae Agapetus	Rhag					0	4
Glossosoma boltoni Curtis	Glbo			2	66		
Lepidostoma hirtum (Fabricius)	Lehi					3	0
Anabolia nervosa Curtis	Anne					9	0
Agapetus fuscipes Curtis	Agfu			1	11		
Psychomyia pusilla (Fabricius)	Pspu			7	0		
Number of taxa		18	25	18	17	21	26
Number of individuals		266	202	829	1196	930	1087

Table 2-7. List of Chironomidae present in the slow (A) and fast (B) reaches of the River Etive.

Taxa	OTU code	A	B
Tanypodinae			
Ablabesmyia annulata group		2	0
Paramerina		5	2
Trissopelopia		2	6
Nilotanypus		0	1
Macropelopia		1	0
Orthocladiinae			
Cricotopus		7	21
Heterotanytarsus		1	0
Thienemanniella		2	0
Tventenia		2	10
Orthocladiinae Genus II		1	0
Chironominae			
Virgatanytarsus		0	1
Tanytarsus		6	4
Rheotanytarsus		5	1
Total		11	6

Reach preferences of taxa

Correlation between deep and shallow section community structure was tested by the non-parametric (G)amma Test on a contingency table based on table 2-6 . For the R. Etive communities correlation was moderate $G = 0.59$, $P < 0.0001$, at the Duneaton Water the correlation was weaker $G = 0.45$, $P < 0.005$ but at the Blane Water the correlation was particularly strong, $G = 0.67$, $P < 0.001$. Note however that for the Blane Water the Chironomidae were excluded from the analysis as their numbers were only estimates.

River Etive

Invertebrates from both the deep and shallow reaches were more typical of riffle fauna than pool. Occurrence of animals was low, (468 specimens collected) reflecting the poor nutrient status of the river. A total of 38 taxa was recorded from the two reaches, 29 taxa from the deep (pool) reach and 32 from the shallow (riffle) (note Chironomidae were identified to genus level where possible for Etive samples but not for the other sites, increasing the number of taxa). A biodiversity index of similarity was calculated for the two reaches PSc = 52% (Cowan & Peckarsky 1990). This indicates only a medium degree of similarity between the two reaches. OTU were tested for differences in distribution between the two reaches using the Mann-Whitney U test. Only two OTU showed a statistically significant preference for either reach. Median abundance of *Hydroptila* spp was greatest in the pool reach, ($W = 860.0$, $P<0.001$ adjusted for ties) while *Caenis rivulorum* median abundance was greatest in the riffle reach ($W = 610$, $P<0.05$ adjusted for ties).

Duneaton Water

In total 2017 animals were collected. A total of 47 taxa was recorded from the two reaches, 21 taxa from the deep reach and 26 from the shallow. OTUs were tested for differences in frequency distribution between the two reaches using the Mann-Whitney U test. The abundance of benthic invertebrates was compared between the shallow (run) and deep (pool) using the Mann Whitney U test. The test was applicable to 19 OTU (other OTUs had extremely low abundances and were excluded). *Ecdyonurus* had a median preference for riffles ($P<0.001$). Other Ephemeroptera, *Baetis rhodani* and *Ephemerella ignita* also showed a strong preference for the run reach ($P<0.05$). Both species of Leuctridae showed a preference for the run reach as did the riffle beetle larvae *Limnius volkmari* ($P<0.05$). The Tipulidae also showed a strong preference for the run reach ($P<0.05$). The only OTU with a significant preference for the pool was *Oulimnius tuberculatus* ($P<0.05$).

Blane Water

Excluding chironomids, a total of 2025 animals was collected. In both reaches chironomids were estimated at greater than 1000 individuals and not identified further. A total of 35 taxa was recorded from the two reaches, 18 taxa from the deep (run) reach and 17 from the shallow (riffle). OTUs were tested for differences in distribution between the two reaches using the Mann-Whitney U test. The abundance of benthic invertebrates was compared between the riffle and run using the Mann Whitney U test. Other OTUs had extremely low abundances and were excluded. *Baetis rhodani* and *Glossoma boltoni* showed a strong preference for the run reach ($P<0.05$).

2.4 Discussion

This study aimed to relate the physical attributes of deep and shallow reaches to a subjective assessment of their habitat type. To confirm actual habitat distinctiveness between reaches, I assessed the biological differences between the reaches. It was possible to differentiate between sites using physical variables. Some species did show preferences for either deep or shallow reaches, reflecting observations previously made in the literature.

2.4.1 Physical character of the Reaches

At all three sites it was possible to differentiate between riffle, run or pool using the range of depth and velocity in the reaches. Froude number was the best indicator of all. Jowett's rule did show some of the reaches to be runs which was not expected and did not conform to the visual assessment of the reaches; I chose the deep reaches as pools and shallow reaches as riffles. Noteworthy was the ability of Jowett's rule to differentiate between the deep and shallow reaches of the River Etive. As mentioned earlier the river is rithron dominated and does not have a classic riffle pool sequence. The sites on which Jowett based his work included boulder strewn reaches, which may have been similar to the R. Etive (Jowett 1993). Alternatively this may be the result of a sampling error on my part as the pool and riffle could not be differentiated using the larger data set which included sampling points which had non significant velocity profiles.

There are consistent differences between all the reaches which suggest that the suite of physical variables measured did differentiate between them. With the exception of the Blane, the sites showed the deeper reaches to be depositional and the shallower reaches to be relatively erosional. This pattern is consistent with the definition of pools as depositional zones and riffles as erosional zones. The fact that the deep reach of the Blane does not follow this pattern would suggest that it is a run. The water in both reaches of each river was predominately turbulent with laminar flow being rare. This is also consistent with the findings of other studies and the predictions of geomorphologists.

Others using a more descriptive classification of near bed flows have suggested that the habitat classifications of pool, riffle and run do not necessarily apply to near bed habitats as all their near bed flow categories were recorded in each class (Young 1993). It is perhaps better to view these habitat classes as aggregates of smaller habitat units especially as they do have some biological significance, see below.

2.4.2 Biological character of the Reaches

Diversity

The riffle reaches supported greater numbers of taxa than the deep reaches conforming with the norm in other studies, see introduction for references (reach 1.1. paragraph 9); however again the Blane was an exception.

Species composition

Ephemeroptera and Chironomidae dominated the fauna at all sites a situation noted in previous comprehensive surveys of the summer fauna of highland rivers, (Morgan & Egglishaw 1966). The methods employed by Morgan and Egglishaw were similar to the one I used, being a combination of disturbing sediment and stone scrubbing adding a degree of certainty to the comparison. This result reflects the seasonality in relative abundance of taxa as the same survey found the spring fauna to be dominated by Plecoptera and Ephemeroptera and suggests applying data gathered on benthic commmunity structure and composition in one season to other seasons is potentially misleading.

Hydroptilidae were detected in the River Etive in high numbers but not at the other sites. This may again reflect a seasonal effect as the R. Etive was sampled later in the summer, in August, than the other two sites. This hypothesis is supported by a seasonal study on invertebrate fauna in another Scottish river, Shelligan Burn a tributary of the River Almond, where Hydroptilidae were detected in low numbers until August when their numbers increased (Egglishaw & Mackay 1966). As the taxon is known to occur in both the Blane Water and the Duneaton Water (SEPA pers comm.) it would seem likely that the effect is seasonal rather than the R. Etive being a site of particular suitability for the taxon. Further evidence is that during their sampling of the R. Etive Morgan & Egglishaw (1966) found the taxon in low numbers; their sampling was in July, the same period the my sites were sampled.

Caseless caddis were represented by more species in all rivers than cased; the Blane did have the highest number of cased species. Again this mirrors the findings of other workers (Armitage & Gunn 1996; Morgan & Egglishaw 1966) who also found as I did that the Orthocladiinae dominated the chironomid fauna. The Etive was the most extreme in this respect with the largest number of caseless caddis species represented of all the rivers and probably reflects the instability of depositional habitat within the site; the larger boulders and lack of small substrate elements at the site attest to this. Cased caddis do tend to require more stable conditions on the whole. Both the Blane and the Duneaton had greater amounts of finer substrate, no or few boulders and greater numbers of cased caddis species than the Etive. Using riffles, pools and rock outcrops as mesoscale habitat units others have identified functionally distinct caddisfly communities (Huryn & Wallace 1988). There is some evidence from this study that this might be occurring here too. The *Hydropsyche* larvae preferred the fast reaches, *Anabolia nervosa* and *Glossoma boltoni* favoured the slower reaches and there is the possible link between *Hydroptila* spp. and boulders. Some of these relationships are not statistically significant and the functional feeding strategies of some of the species need to be clarified.

Other unique aspects of the R. Etive species assemblage is the absence of both Mollusca and crustacean macroinvertebrates which is likely to be a product of the underlying geology as is the case with the high numbers of Mollusca in the Blane Water (Egglishaw & Morgan 1965). Macan (1977) divides the British freshwater molluscs into two major groups based on their preference for hard or soft waters. Calcium which is needed to form shells is the underlying determinant for separating the two groups and is an element which is likely to be in short supply at the R. Etive.

Individual species responses in relation to site specific factors

A number of species showed preferences for either deep or shallow reaches, suggesting that for some invertebrates at least, the different types of reaches represent habitat units. How Hydroptila species avoid getting washed out of the Etive system is interesting to ponder; it may be that their small size allows them to seek refuge in the filamentous algae on which they are known to feed. I observed in the field that the greatest amounts of filamentous algae were on boulder tops, submerged in the deep reach, a most stable substrate. Alternatively the preference of Hydroptila species for the deep reach for the R.Etive may be explained by the need of this taxon for very fine sand grains to form cases during it's last instar (Wallace 1981). Sand did occur with greater frequency in the deep reach of the river. Hydroptilidae also had a significant preference for pools in the Almond Water (Egglishaw & Mackay 1966). *Caenis rivulorum* the only other animal found to have a preference in the R.Etive was found by Armitage (1976) to prefer the 'intermediate' (0.2-0.6 ms^{-1}) reaches of the R. Tees, which has comparable velocities to the Etive riffle reach.

The preferences exhibited by both mayfly and stonefly in the Duneaton water (run) for faster reaches have been observed elsewhere in British rivers, in the Tees (riffle), the Afon Hirnant (riffle) (Hynes *et al.* 1976) and the Almond (riffle), although the reflected patterns were not perfect. In the Tees, *Leuctra fusca* and *Ecdyonurus dispar* were among some of the few taxa to show no preferences, whereas in the Almond *Ecdyonurus* spp. were in greatest abundances in the pools in April and the riffles in September. Morgan & Egglishaw (1966) believed this seasonal variation was due to different preferences being exhibited either by *Ecdyonurus* spp. instars or species. Alternatively they believed that pre-emergence behaviour altered the animals habitat choice. Again it is interesting to note that *Limnius volckmari* had a preference for the pools in the Tees which were of similar velocity range as the run in the Duneaton water to which it was also partial (Rosillon 1988).

Contrary to its previously reported preferences I found Tipulidae to occur most frequently in the riffle of the Blane which is difficult to explain. Easier to explain, yet equally at odds with previous studies, is the preference exhibited by *Baetis rhodani* for the run reach. An extensive study covering a greater number of rivers found *Baetis* species indicative of riffles (Harper *et al.* 1998). This trend can be seen in the Duneaton Water where *Baetis rhodani* also showed a preference for the run. The fact that the animal occurred with greater frequency in the run of the Blane Water suggests that it was avoiding the riffle reach of the stream (the run reach was immediately downstream of the riffle). Drift rates of baetid mayfly have been experimentally shown to be greater during spates (Lancaster 1992). Harper's study (1998) also showed *Caenis* species as being indicative of silted riffles and runs whereas my data suggests they occur preferentially in the shallow reaches of the R. Etive.

Some OTUs showed differential preferences for the reach types present at different sites. Based on substrate type the R. Etive experiences the highest shear forces of the three rivers with the Duneaton Water having the next highest. As the substrate was only sampled to a depth of 10cm, composition of the armoured layer only was measured. Hence the substrate types reflect the rivers' recent past only. Any larger substrate elements will have been buried by more minor spates. In this context the R. Etive is likely to have more intense spates than the other two rivers, as one would expect from the steep gradients in the catchment. I suggest that the intensity of recent disturbance at the three sites, as experienced by invertebrates is most intense in the R. Etive, least intense in the Blane Water and intermediate at the Duneaton Water. This measure does not differentiate between disturbance events with high frequency, low force and low frequency, high intensity. There is also the possibility that the armoured layer, if compacted by low intensity spates becomes more resistant to entrainment and this index based solely on substrate type could underestimate the resistance of the substrate. This is most likely at the Blane where the substrate appeared quite compact.

2.5. Conclusions

2.5.1 Physical study

- Jowett's rule accurately differentiated between riffles and pools; it also identified the deep reach of the Blane as a run highlighting the danger of choosing a site during one set of flow conditions and sampling under another. It also classified the R.Etive reaches into pool and riffle although geomorphologists would disagree on the grounds of the highly erosional nature of the stream and ecologists on the basis of the predominantly riffle type fauna of the 'pool'. In rivers of high slope the rule should probably be applied with caution if at all.

- Separating pools, runs and riffles on a subjective observational basis is insufficient on the evidence of this study. Some measurements of velocity and depth need to be performed.

- A large proportion of the physical variability between the riffles and pools was consistent between sites. Further the mixture of substrate in the deep and shallow reaches suggested that they were depositional and erosional zones respectively.

- Flow was turbulent in all reaches with a measurable laminar sub-layer being rare. I conclude that at the substrate surface oxygen is unlikely to be a limiting factor.

2.5.2 Biological study

- Each river had a unique assemblage of invertebrates, although there was a large degree of overlap in composition between sites. Differences could be explained by comparing my results with previous studies on the distribution of invertebrates in relation to geology and water chemistry.

- Riffles supported a greater diversity of species than the pools although the assemblage of species in both pools and riffles were not sufficiently different to separate them using TWINSPAN.

- Some species showed preferences for either deep or shallow reaches, these preferences were usually site specific and reflected a large number of local factors, but velocity and substrate type are probably the most important.

- Based on the physical and biological data it seems clear that riffles and pools represent local combinations of physical habitat conditions which alter temporally and are fundamental to maintaining the diversity of macroinvertebrates in Scottish rivers.

- Most taxa can survive outwith their preferred habitat unit (either riffle or pool) suggesting that their own physical habitat preferences are acting on a smaller physical scale.
- The species that make up the assemblages are likely to exhibit preferences for the environmental variables associated with pools and riffles e.g. depth, velocity, substrate type etc. The evidence also suggests that these variables are fundamental to niche separation among the species present. This is explored in the next two chapters.

Chapter 3: Benthic invertebrate community ordination

3.1 Introduction

3.1.1 Outline

The purpose of this chapter is to examine the distribution of benthic invertebrates in relation to hydraulic environmental variables at a finer physical scale than the previous chapter. The data presented here reflect the habitat complexity on an intra-reach scale and gives some indication of inter-river variation. The analysis consists of two stages: the first attempts to find structures in the invertebrate community e.g. associations or clumps of species from samples within the same river. The second stage tries to relate community organisation to environmental factors. By using ordination and cluster analysis it was hoped to identify groups of invertebrate species with indicator species which have similar flow requirements.

3.1.2 Physical patchiness

The design of a program monitoring the ecohydrological health of rivers could successfully incorporate the results of such analysis. By exploring species distribution independently of environmental variables in the first instance the two stage process has the advantage, of following (Pringle *et al.* 1988) advice - *'that variability among patches in lotic systems be viewed as valuable information rather than statistical noise to be overcome by manipulating sampling protocols'*.

Hildrew & Giller (1994) explored the link between habitat patchiness, scale, disturbance and the stream benthos. They made the link between the concept of habitat template (the river: Southwood 1988) and benthos, pointing out that although the river habitat is heterogeneous, clumping or aggregation of similar types of habitat is common:

"Undoubtedly the major architects of physical patchiness in streams are the forces of flow. Flow is scale-dependent, being heterogeneous and 'aggregated' (i.e. different habitat 'patches' have different average flow characteristics) at different spatial scales ranging from the sub-millimetre to whole river reaches or entire drainage networks. "

3.1.3 Spatial aggregations

The more obvious aggregations include riffles and pools (which were the subject of the previous chapter), but within these there occur smaller habitat units. In a diagram illustrating scale effects (Hildrew & Giller 1994) showed fine gravel patches, moss on boulders, transverse bar of cobbles and sand and silt over cobbles as aggregate units at the '*microhabit*' scale (10^{-1} m). By using cluster and ordination methods it might be possible to reflect this pattern, by clumping species together that occur in the same habitat aggregates. Although the quadrat size used to sample invertebrates is on a comparable scale (sample area = 0.0625 m^2) to the microhabit scale, in my study there was the possibility of sampling across two or more discrete habitat units, due to the random choice of sampling points. All physical variables were measured on continuous or integer scales so that taxa responses to variables could be observed even when more than one microhabit was sampled.

3.1.4 Assessment of the ecohydrological health of rivers

Research in this area is driven by two forces, firstly the pure scientific interest in niche separation and habitat patchiness in rivers and secondly the development of conservation and monitoring strategies for river health using responses of benthic invertebrates to flow in regulated rivers. The 1999 draft of the EC Water Frameworks Directive (19 February 1999) underlines the potential importance of this type of study. The draft requires member countries to identify high quality reference sites for surface waters, including rivers (Annex II section 1.3, paragraph iv). Ecological status is to be defined using biological and hydromorphological elements. The hydromorphological elements are defined as those which support the biological element and include hydrological regime, river continuity and morphological conditions; depth, width, structure of bed and substrate type (Annex V section 1.1.1). Under the directive these pristine rivers would form a standard all other rivers would have to reach. In preparation for this legislation SEPA are currently trialing **I**nstream **F**low **I**ncremental **M**ethodology (IFIM, (Bovee 1982)) and its associated computer programme **P**hysical **Hab**itat **Sim**ulation (PHABSIM). PHABSIM is one of a number of models which evaluate riverine physical habitat, specifically it models the available habitat for aquatic species at different discharges (Johnson & Law 1995). Its successful application elsewhere as a means of estimating instream habitat make it a suitable candidate (e.g. (Armour & Taylor 1991) reports 616 applications of IFIM up to the early 1990s in the United States alone). Both the methodology and the program have mainly been applied to salmonid fisheries management (Armour & Taylor 1991; Johnson *et al.* 1995; Jowett 1998; Strevens 1999). This list of references is not by any means exhaustive: rather it is intended to give the reader a representation of the work being carried out on different continents.

IFIM has been used to estimate habitat suitability curves for benthic invertebrates (Jowett *et al.* 1991) and PHABSIM predictions of increased habitat availability for benthic invertebrates in artificial riffles have shown positive and significant correlations with actual measures of increased biodiversity (Gore *et al.* 1998). By using a variant of IFIM developed for collecting data on benthic invertebrates (Jowett *et al.* 1991) in the work reported here, it is hoped to make the work comparable to other similar studies.

When using PHABSIM there can be a conflict between the flow requirements of different species. One aspect of this study is to attempt to find clusters or guilds of species associated with combinations of flow variables which simplifies this management problem. This technique has been successfully applied to the management of fish stocks (Jowett & Richardson 1995).

Criticism can be levelled at PHABSIM on a number of fronts, probably the most fundamental being that annual flows for a river are determined from one or few 'snap-shot' IFIM studies which only reflect the fauna's preferences at the time of sampling. Another serious problem is that PHABSIM assumes *'that target organisms have specific microhabitat preferences and the ability to move to areas of suitable hydraulic conditions in response to changes in stream discharge'* (Layzer & Madison 1995). Although this is obviously the case for invertebrates which end up in flow refugia during spates (Lancaster & Hildrew 1993b), as Layzer and Madison point out these assumptions do not apply to sessile or slow moving invertebrates e.g. Mollusca. (they also point out that their study organism, freshwater mussels, appears to have different flow preferences at different discharges). Neither does PHABSIM address the importance of disturbance flood events which redistribute and alter the species composition of riverine invertebrate communities (Boulton *et al.* 1992; Brooks & Boulton 1991; Cobb *et al.* 1992; Dudgeon 1993; Hildrew & Giller 1994).

The aims of this chapter are to test the structure of the benthic invertebrate community at the surber sample scale, identify any aggregations in the distribution of taxa and estimate the influence of flow variables on the variation in community structure using multivariate analysis. The hypothesis is that the distribution of benthic invertebrates should be clumped and that flow variables should describe a large amount of the variation. The interrelations between the environmental variables are described in this context.

By addressing these questions PHABSIM is also tested indirectly, as it assumes that benthic invertebrates are responding to flow variables at this scale, in a predictable manner.

3.2 Methods

3.2.1 Data Collection and Dataset Structures

Collection methods for data examined here are described in the previous chapter. For each river data from both reaches were amalgamated into a matrix of taxa by sites, and a second matrix containing environmental variable by site data. For each river the ordination was attempted using an environmental variable data set which contained variables derived from velocity profiles.

The profiles were measured at all points where invertebrates were sampled. For each profile, velocity should show a linear relationship with log depth if a full developed boundary layer exists and the layer is not disturbed by gross alterations in water movement, e.g. a velocity profile taken downstream of a semi submerged boulder may show a log linear relationship at the depths above the boulder but back edding may distort the profile lower down. Not all profiles had significant R^2 values and these were discarded as near bed flow variables could not be calculated from them being dependent on the log linear relationship between depth and velocity being intact, see chapter 2.2.4 and Annexes II and III. It has been suggested that some data could be salvaged from these profiles. The mean water column velocity was calculated for these points from the profiles allowing their inclusion in the 'larger dataset', see below.

An alternative method of salvaging data from the profile was to use them to estimate turbulence above the bed, using their deviation from the predicted log-normal relationship as a turbulence surrogate. Given that turbulence at the bed is the factor of most interest, as that is where the animals are and, not turbulence further up the water column, the use of the profiles in this way was not suitable.

Two data sets for each river were now analysed. The dataset containing sampling points for which velocity profiles were intact and a second larger dataset which included all sampling points where invertebrates were sampled. The larger datasets contained a more limited array of environmental variables; mean water column velocity, depth, % sand, % fine gravel, % gravel, % cobble, % boulder and % bed rock. The smaller datasets with significant velocity profiles also contained these measures.

Where the smaller data sets proved unsuitable the larger parent data set was used instead, see section 3.3.1. For the R. Etive where many taxa occurred in few samples the data set excluded taxa occurring in less than 5 samples.

3.2.2 Analysis procedure

The production of an ordination analysis requires refinements to the input data which influences the final result as does the structure of the data sets involved. Initially a TWINSPAN analysis was carried out on the data from each site and the groups overlaid in a Detrended Correspondence Analysis (DCA) taxa scatter plot. As TWINSPAN and DCA both use the same algorithm to order a species by site matrix this process is acceptable. This allows TWINSPAN groups to be visualised in an ordination diagram as opposed to a dendogram aiding interpretation and allowing comparison with constrained ordinations (see last paragraph for an expanded explanation). No TWINSPAN analysis was performed on the Blane Water data because DCA showed the length of the environmental gradient to be short suggesting taxa were exhibiting linear responses to the environment. As TWINSPAN is based on a unimodal model it was not applicable.

Outlined below are the methods used to derive the final ordinations, highlighting the peculiarities of each river's data set and the refinements made. For each site a DCA was carried out initially to measure the length of the environmental gradient as suggested by the CANOCO computer program help (ter Braak 1997, 1998). Depending on the length of the gradient, either a unimodal (gradient >3-4 s.d.) or linear (gradient <3 s.d.) based ordination technique was used. The results of each ordination were interpreted with the aid of the explanations given in the CANOCO manual, chapter 6 (ter Braak & Smilauer 1998) and adjusted where necessary.

Constrained ordination techniques (Canonical Correspondence Analysis (CCA), Redundancy Analysis (RDA)) have been criticised for being potentially misleading (McCune 1997), so some clarification of their purpose is useful. Other ordination techniques which are not constrained describe community structure e.g. DCA scatter plots will clump species together which co-occur. Constrained ordination techniques do not: primarily they relate species distribution to environmental variables. If one wishes to relate community structure to environmental variables one should apply an indirect gradient analysis and subsequently relate this ordination to environmental variables, e.g. DCA and superimpose the environmental variables on top of a scatter diagram. Jongman *et al.* (1988) suggests a number of methods for relating unconstrained ordinations to environmental variables. Another useful alternative is to first carry out an unconstrained analysis and compare it to a constrained one as is the case here., Here I compared DCA to CCA, though there has been the criticism that DCA should only be compared to DCCA, presumably on the basis that both are detrended. Detrending is a remedial tool for fixing the 'arch effect' in ordinations (Jongman *et al*, 1988). It was not necessary to apply it to the CCA~~'~~s here. A dataset which produces an arch effect when processed by unconstrained ordination does not necessarily do so when the ordination is constrained (Jongman *et al* 1988). That was the case here. The arch effect occurs for two fundamentally different reasons in CA and CCA. In CCA diagrams it is usually caused by the inclusion of too many environmental variables whereas in CA it a mathematical artifact caused by the structure of the species by samples data set. Although detrending alters the position of points in an ordination, their relative positions to one another should remain relatively constant making it feasible to compare between ordinations.

River Etive

The length of the environmental gradient as determined by DCA was long (Axis 1 = 4.135 s.d.), so a unimodal based analysis was used i.e. CCA. The best four explanatory variables were chosen using forward selection. The variables % bed rock (1 sample) , % fine gravel (6 samples) and % sand (1 sample) were not used in the analysis as all occurred in very few samples. They were included as passive variables only. The taxon Oxythira was used passively after demonstrating a much stronger relationship with axis 1 & 2 than all the other species.

Duneaton Water

The length of the environmental gradient as determined by DCA for the larger data set was between 3 and 4 s.d. (Axis 1 = 3.05 s.d.), the cut off point for selecting either a linear or a unimodal based analysis. In this instance either a unimodal or linear method is applicable, CCA was chosen. Log transformation of the species data reduced the variance in the species data explained by the first two ordination axes to 11.4% and the explained variance in the fitted species data from 78.7% and was not applied in the final analysis. Extreme values were detected for 7 samples, but all 'really belong to the population' (ter Braak & Smilauer 1998, p118) so these outliers remained in the analysis. Of the possible variables used in the analysis, both % composition of boulder and % composition of fine gravel were excluded as both substrate types were found very infrequently (n = 2 and n = 6 samples respectively) causing them to appear to be collinear with the variable % composition of sand. None of the remaining variables had a variance inflation factor >20 indicating that they all had a unique contribution to the canonical ordination.

Blane

A DCA of the Blane Water species data set (40 useable samples) showed the gradient length to be less than 3 s.d. (2.505) suggesting a linear as opposed to a unimodal model was most applicable e.g. redundancy analysis (RDA). RDA analysis was not significant for all canonical axes taken together (Monto Carlo test full model p = 0.085) although the first axis was significant (Monto Carlo test p = 0.015). Constraining the ordination with environmental variables was not significant, so the species data are presented in an indirect gradient analysis ordination, Principal Components Analysis (PCA). Four samples had extreme values for some of the environmental variables but did not reflect any detectable mistakes in data collection so they were not removed from the analysis.

3.3 Results

3.3.1 Suitability of data sets

For all sites, the data subsets containing variables derived from velocity profiles produced ordinations with no significant canonical axes (Monto Carlo Permutation test $p > 0.05$), see table 3.1.

Table 3-1, Eigenvalues and their significance from ordinations performed using parameters derived from velocity profiles as environmental variables. For the Duneaton Water and River Etive the ordinations were CCA, for the Blane Water the ordination was an RDA. Permutation tests were Monto Carlo tests carried out using 199 randomly seeded runs.

River	Axis 1			All canonical Axis		
	Eigenvalue	F-ratio	P-value	Sum of all eigenvalues	F-ratio	P-value
Blane Water	0.134	3.875	0.91	0.185	0.566	0.88
Duneaton Water	0.141	1.951	0.665	0.539	0.997	0.435
River Etive	0.133	2.003	0.33	0.45	1.056	0.345

3.3.2 River Etive

The DCA scatter plot (figure 3-1) shows two major groups as split by TWINSPAN on its first iteration (TWINSPAN eigenvalue = 0.705). Further iterations produced splits which had low eigenvalues and were not used (0.350 or less).

Monto Carlo tests of the first canonical axis of the CCA and all the canonical axes together were significant (p = 0.005, F-ratio 3.516 and 2.361 respectively). The biplot (Figure 3-2) based on the first two canonical axes explains 11.3% of the variance in the species data and 67.4% of the variance in the fitted species data.

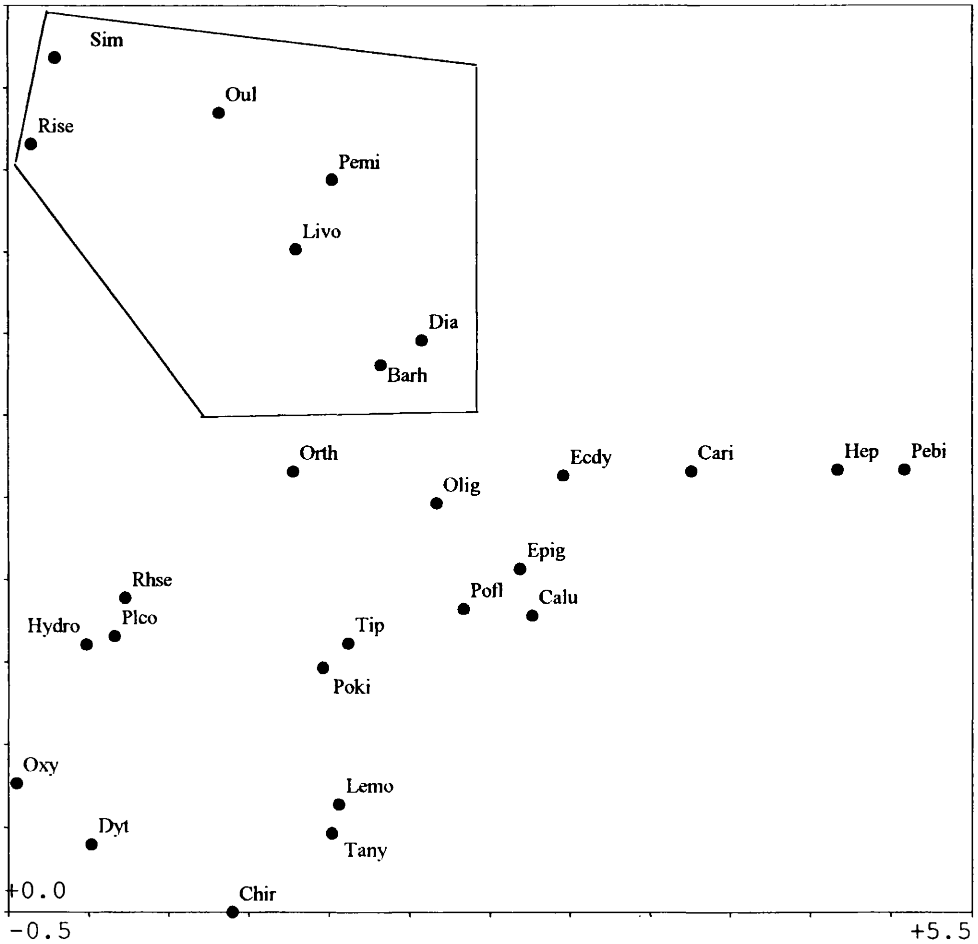


Figure 3-1 Etive DCA. TWINSPAN group A is enclosed by the polygon, all other taxa are in Group B. See chapter 2 tables 2-6, 2-7 for a key to the species codes.

Axis 1 (eigenvalue 0.38) can be interpreted as a microhabitat gradient from erosional to depositional conditions. Velocity and % cover of cobble are most strongly correlated with Axis 1 (weighted correlation 0.69 and 0.41 respectively). Depth and % cover of boulders are both negatively correlated with Axis 1. Axis 2 (eigenvalue 0.24) is most strongly correlated with % cover of boulder and cobble. The coarser material, boulder, is unusually associated with slow flows, in reality boulders were found throughout both sections but only in the deeper, slower areas, where they remained submerged, and available to invertebrates. Only submerged boulders were sampled.

The smaller TWINSPAN group members are scattered throughout the right hand side of the CCA diagram. Mayfly and stonefly species occur almost exclusively on the right hand side of the CCA diagram as does the riffle beetle larvae *Limnius volckmari*. To the right of the centre of the diagram are Trichoptera larvae which require stable substrates on which they can construct their filter nets. The left hand side of the CCA plot is dominated by detritivorous Chironominae, Tanypodinae, Tipulidae and Oligochaeta and the tiny Trichopteran genera *Hydroptila* and *Oxyethira*. These taxa have known preferences for depositional areas, either for feeding or case building material (Hynes 1972; Wallace *et al.* 1990). The presence of Orthocladiinae larvae in samples with higher percentages of cobble reflects a general trend within the Chironomidae. Orthocladiinae prefer large substrate elements to the Chironominae and Tanypodinae (Williams & Feltmate 1994). The Simuliidae were present at extremely high velocities. Representatives of both TWINSPAN groups occurred in each stretch, with only two OTUs showed a strong preference for either deep or shallow stretches. Scattered throughout the diagram are predators. The only cased caddis present were members of the *Hydroptilidae* which are extremely small. Larger sized cased caddis species were notable by their absence. Hence, the CCA ordination showed that the observed differences in invertebrate occurrence could potentially be functionally related to differences in habitat conditions which were paralleled in the literature.

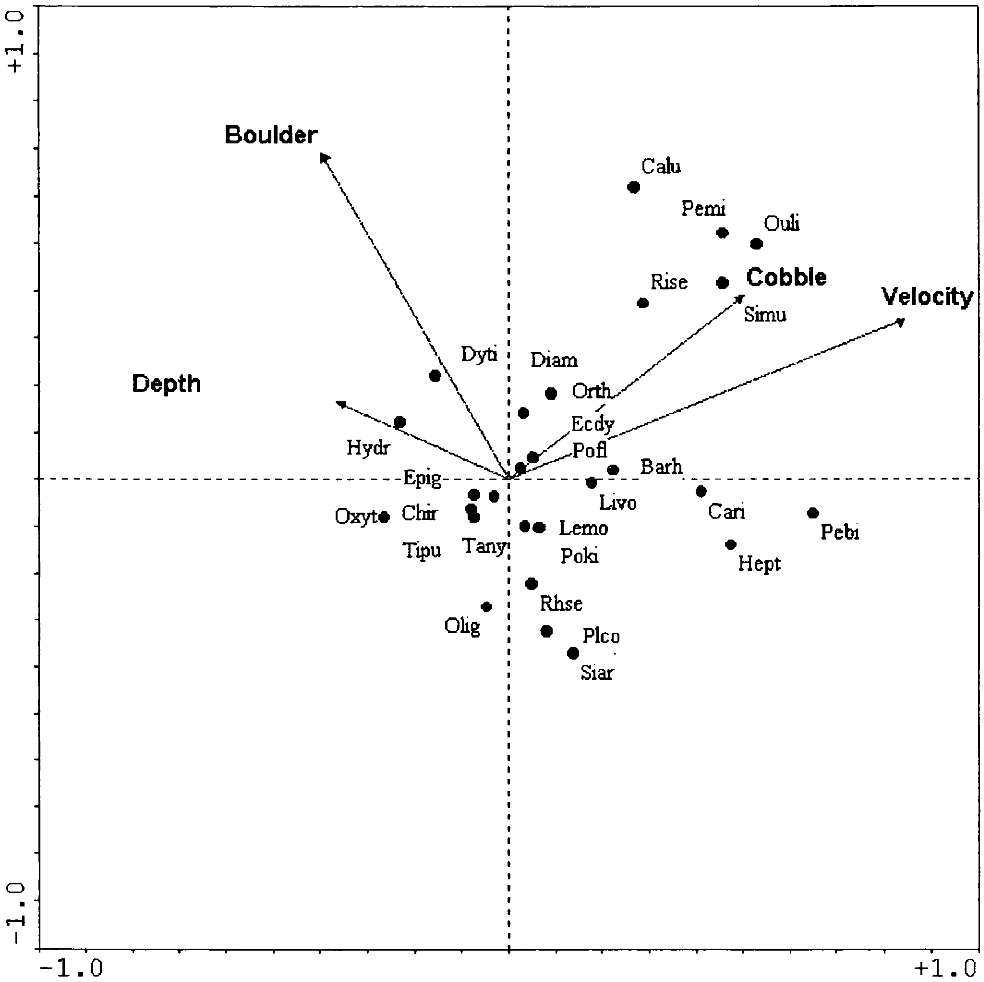


Figure 3-2, CCA species-environment biplot for the R. Etive data. Variance added (λk) for environmental variables: Velocity 0.32 (P = 0.005), Boulder 0.25(P = 0.005), Cobble 0.19(P = 0.015), Depth 0.15(P = 0.045), Gravel was not significant and was eliminated from the ordination. Only OTUs with an occurrence greater than 5 were used in the analysis. OTU codes are give in table 1-6 with the exception of the Chironomidae which were amalgamated in to subfamilies: Chironominae (Chir), Orthocladiinae (Orth), Tanypodinae (Tany) and Diamesinae (Diam).

3.3.3 Duneaton Water

The DCA scatter plot below (Figure 3-3) shows two major groups as split by TWINSPAN (TWINSPAN eigenvalue = 0.784). Further splits by TWINSPAN had low eigenvalues and were not used (0.345 or less).

For the final CCA, Monto Carlo tests of the first canonical axis and all the canonical axis together were significant (p = 0.005, F-ratio = 7.373, 3.080 respectively). The analysis used 5 environmental variables and orientated 28 species which occurred 353 times in the data set. The variance in the species data explained by the first two ordination axes was 19.4% and the explained variance in the fitted species data from was 67.7%.

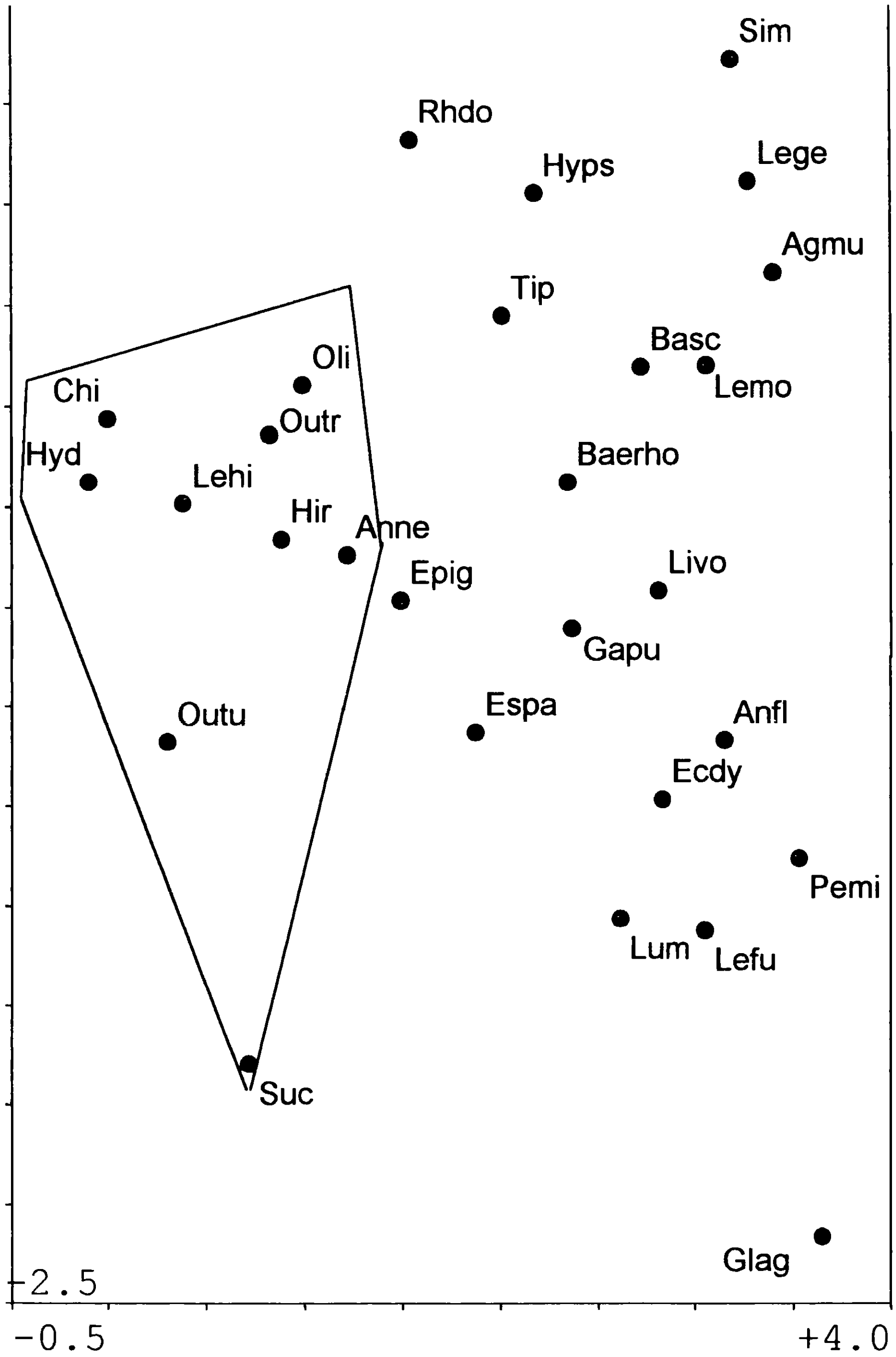


Figure 3-3, Duneaton Water DCA with TWINSPAN groups overlaid. Group A is enclosed in the polygon, group B includes all other taxa. See table 1-6 for OTU codes.

Table 3-2, Weighted correlation matrix (weight = sample total) for environmental variables and Axis 1 and 2 of the canonical ordination used in the R. Etive analysis.

	Mean Weighted	Standard deviation	Axis 1	Axis 2	% Boulder	% Cobble	Mean Velocity	Depth
% Boulder	33.00	44.00	-0.3238	0.5370	1.0000			
% Cobble	14.00	24.00	0.4099	0.3029	-0.3983	1.0000		
Mean velocity	0.23	0.19	0.6896	0.2642	0.1243	0.2679	1.0000	
Depth	0.28	0.20	-0.2995	0.1289	0.1764	-0.0192	-0.1335	1.0000

Table 3-3, Weighted correlation matrix (weight = sample total) for environmental variables and Axis 1 and 2 of the canonical ordination used in the Duneaton Water analysis.

	Mean	Standard deviation	Axis 1	Axis 2	Mean Velocity	Depth	% Cobble	% Gravel	% Sand
Mean Velocity	0.24	0.22	-.5962	.3391	1.0000				
Depth	0.17	0.11	-.2617	-.2549	.0967	1.0000			
% Cobble	24.00	31.00	-.4995	.4109	.6931	.0223	1.0000		
% Gravel	53.00	28.00	-.1308	-.5434	-.1309	.2465	-.5496	1.0000	
% Sand	18.00	26.00	.7923	.0926	-.6234	-.2763	-.4968	-.2753	1.000

As can be seen from Table 3-4, velocity is strongly positively correlated with cobble, the larger more stable substrate element at the site, and is negatively correlated with sand. Depth is not strongly negatively correlated with velocity as it often is at other sites. Axis 1 (eigenvalue 0.404) is strongly positively correlated with the % sand in samples and strongly negatively correlated with both mean velocity and % cobble. Axis 2 (eigenvalue 0.175) is most strongly correlated with % gravel (negative) and positively correlated with % cobble and mean velocity. The use of biplot scaling with the focus on inter-species distances as used in the analysis of the Etive data resulted in the species points clustering in the diagram centre making interpretation difficult and the scaling was altered to inter-species scaling using Hill's scaling (ter Braak & Smilauer 1998). The species are grouped along axis 1 and to the left of axis 2 . The Ephemeroptera and Plecoptera occur exclusively on the left hand side of the origin, the other orders are scattered across the diagram depending on the preferences of their composite genera.

TWINSPAN group A members, plotted in the Duneaton Water DCA remain associated with one another in the CCA plot (Figure 3-4). Some group A members are strongly associated with high percentages of sand and independent of other variables and can be found to the right of the diagram; *Succinea,* Hydrocarina, Chironomidae and *Ouliminius tuberculatus*. Closer to the origin, and occurring in samples where velocity and the percentage of cobble would be low, is *Leptistoma hiratum* and Hirundinae. Closer to the origin where the mean of all variables occur are the Oligochaeta and *Gammarus pulex* (which is a group B member). This suggests these two taxa have a either a preference for the mean of all condition measured or are

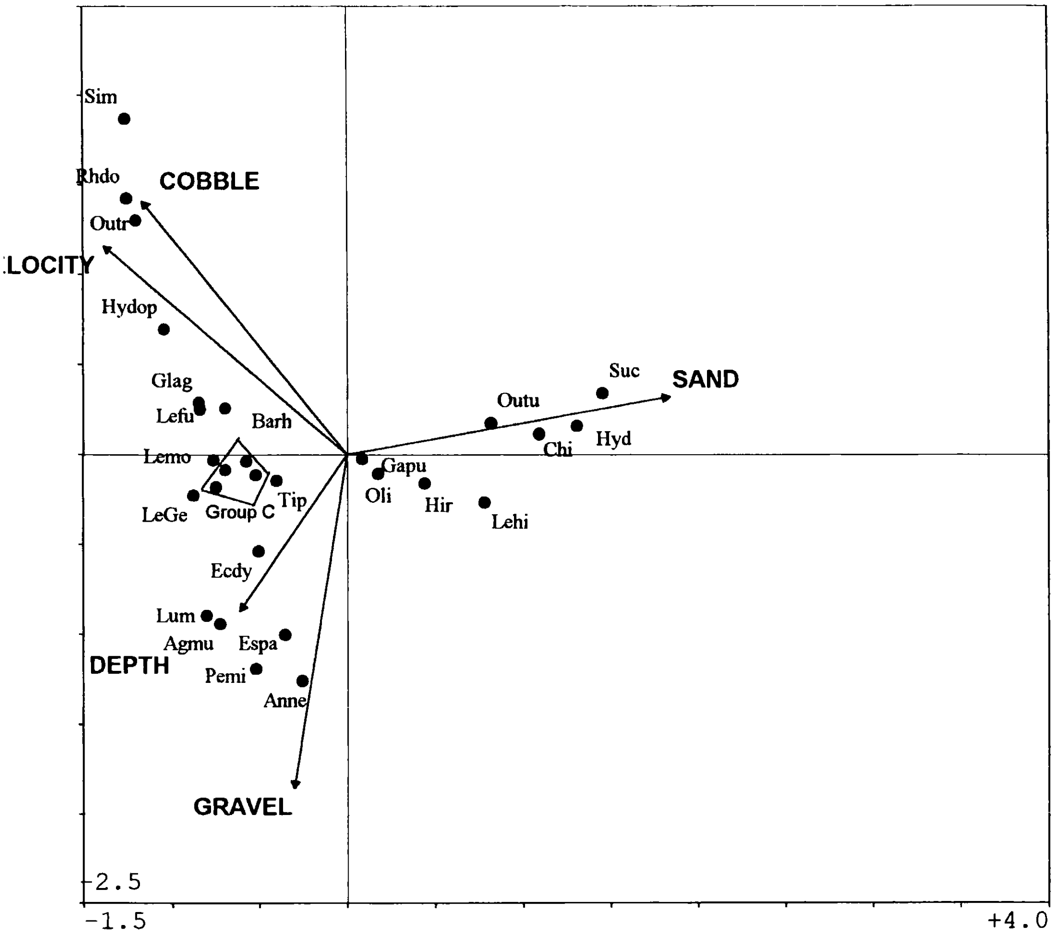


Figure 3-4, Duneaton Water CCA. Group C enclosed by the box includes *E. ignita, B. Scambus, L. volkmari* and *A. fluviatilis.* Variance added by the environmental variables listed in order of their inclusion in the model; variance (λA) values in brackets are the amount of additional variance explained by the inclusion of each variable sand (0.39 p = 0.005), cobble (0.14 p = 0.005), depth (0.09 p = 0.045), gravel (0.06 p = 0.205) and mean water column (mwc) velocity (0.06 p = 0.315).

ubiquitous in their presence. *Anabolia nervosa*, one of only two group A members not closely associated with other group A members in the CCA shows a preference for high % gravel and deep water. The other vagrant is *Oulimnius troglodytes* which has a preference for high % cobble and fast water.

The taxa of group B show a more varied series of interactions with flow variables. At the top left of axis 2 are two taxa, the Simuliidae and *Rhyacophila dorsalis* with a strong affinity for high % of cobble and fast water. The *Hydropsyche* also have a strong preference for fast water but their preference for high % of cobble is less. These 3 taxa can be found close together in the DCA plot. To the left of the origin there is a group with no strong affinity for either velocity or depth. This grouping does prefer samples with less sand and more of the other substrate types, it includes; Glossomatidae (possibly *Agapetus*), *Leuctra* sp., *Baetis rhodani*, *Baetis scambus*, *Ephemerella ignita*, *Ancylus fluviatilis* and the Tipulidae. It is the largest of all the groups. Strongly associated with deep water are the Lumbricidae, *Agraylea multipunctata* and *Esolus parallelepipedus*.

3.3.4 Blane Water

The data used in the PCA covers 19 taxa which occurred, cumulatively 254 times in 40 samples. The variance inflation factors for all environmental variables were low (all < 2) suggesting that the variables are not highly correlated with one another which agrees with their product moment correlations in Table 3-4, all of which were less than 0.5. Depth is positively correlated with both velocity and high percentages of cobble. Velocity is not strongly positively correlated with % cobble as was expected although it is relatively strongly and negatively correlated with % sand.

Table 3-4, Blane environmental variables, weighted mean, standard deviation and product moment correlations.

	Weighted mean	Standard deviation	% Cobble	% Gravel	% Fine gravel	% Sand	Mean Velocity	Depth
% Cobble	7.6038	9.6100	1.0000					
% Gravel	65.8945	27.4497	0.0017	1.0000				
% Fine gravel	6.4284	10.1222	-0.2134	-0.2350	1.0000			
% Sand	12.5732	16.4907	-0.0948	-0.4295	0.1906	1.0000		
Mean Velocity	0.4288	0.3200	-0.0358	-0.0283	0.0347	-0.3751	1.0000	
Depth	0.1421	0.0896	0.2253	-0.2710	0.0713	-0.0177	0.2918	1.0000

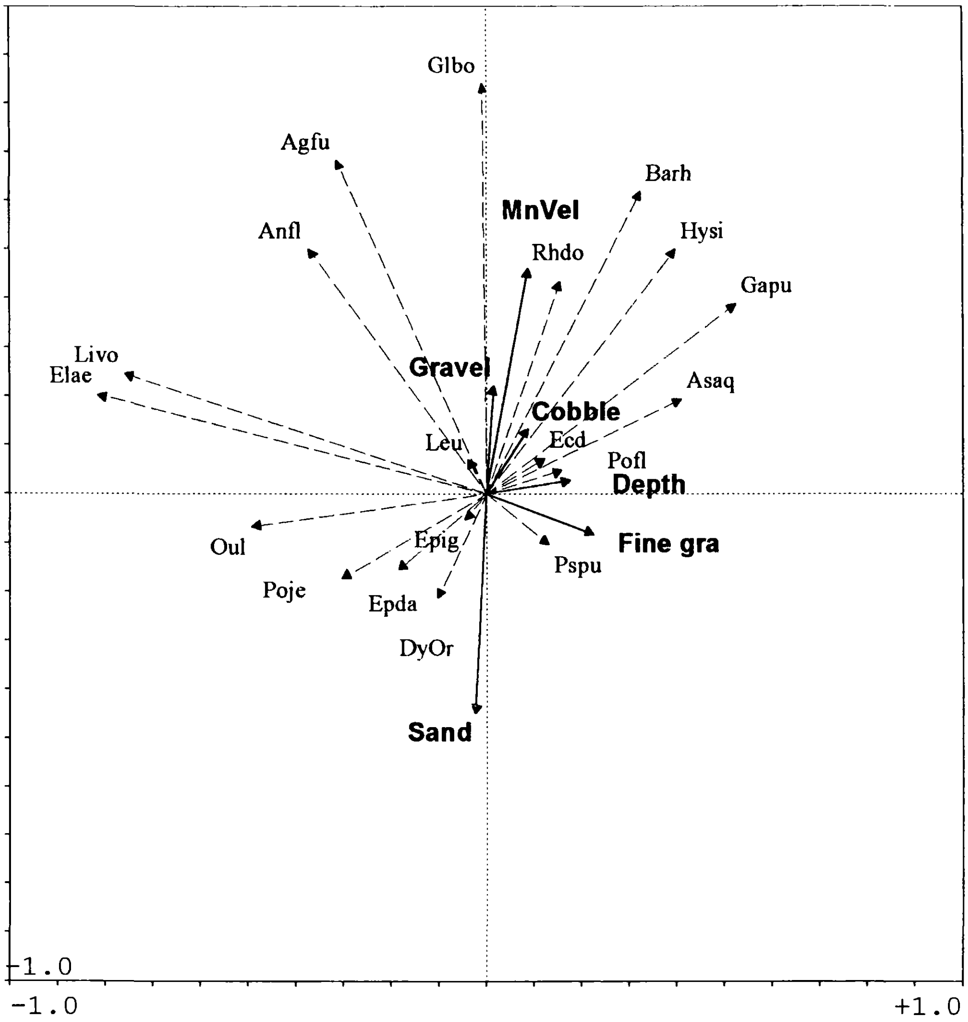


Figure 3-5, Blane PCA correlation biplot with environmental variables imposed over the ordination. Solid arrows = environmental variables, dashed lines = taxa. Scaling focuses on interspecies distances and the ordination diagram displays standardised species data (by dividing by their standard deviation) post transformation, and correlations. The values that can be inferred by the biplot rules are thus correlation coefficients(ter Braak 1997, 1998)

The biplot in Figure 3-5 can be interpreted using the rules given by Jongman *et al* (1987: p127). The arrow for each taxon indicates a vector increasing in the direction of increasing abundance for each species, arrows pointing in the same direction are positively correlated, perpendicular arrows reflect a lack of correlation between the variables represented by the vectors.

The species are scattered throughout the diagram with little grouping apparent. The distribution of *Limnius volckmari* and *Elmis aenea* are closely correlated as are *Ancylus fluviatilis* and *Agapetus fuscipes*. *Glossoma boltoni* increases in the same direction as gravel, as does *Rhyacophila dorsalis* with mean velocity. A group of 3 species with similar distributions are *Baetis rhodani*, *Hydropsyche siltalai* and *Gammarus pulex*. *Potamopyrgus jenkinsi* and *Ephemerella danica* are also similar in distribution.

3.4 Discussion

The constrained ordinations shows that clustering of the invertebrate data was limited to two major groups at the Duneaton water and the R. Etive sites. The flow variables in these constrained ordinations showed strong relationships between some taxa and flow variables. The often observed selective occurrence of macroinvertebrates at either erosional or depositional conditions were also observed here although, as found by Barmuta (1989) community structure appeared more continuous in nature and confirms the view of earlier researchers that the use of substrate as a basis for delimitation bottom fauna may be limited (Thorup 1966). These selective occurrences reflected the preferences of most taxa for slow or fast reaches as observed in the previous chapter.

The implications for IFIM based studies are profound. Although some taxa showed similar responses to flow variables in the different rivers e.g. *Rhyacophila dorsalis* others were inconsistent. This reinforces the argument that data collected at one site should not be used to build a model for other locations. It also highlights that there can be considerable variation in the response of a taxon to flow variables.

Improvements to sampling strategy for future work in this area are suggested and the implications for how we should view the patchy nature of the stream bed are discussed.

Clustering of the taxa data from the Duneaton Water and R. Etive with TWINSPAN split both site communities into two main groups. For each site the composition of the two groups produced was very different, probably reflecting site specific factors. The smaller Duneaton Water group preferred deposition conditions whereas for the R. Etive the smaller group was erosional in nature. One possible criticism of these results is that as both groups contained a mixture of functional feeding groups (Group A from the R. Etive contains Simulliidae and *Baetis rhodani*, respectively a sedentary filter feeder and a swimming deposit feeder (Williams & Feltmate 1994)), it would be expected that such groups would be separated by a cluster analysis on data with sufficient habit resolution.

The limited success of TWINSPAN at splitting the communities into a greater number of intelligible groups could be for one of two main reasons, either the communities are relatively homogenous in composition and spatial distribution or alternatively individual quadrats covered a sufficient range of underlying microhabits that heterogeneity was disguised. Either way this is good news for those using quadrat sampling as a representative measure of invertebrate community structure at a particular site. In future work a sampling program based on smaller quadrat sizes would be expected to yield clearer results as it has been frequently shown that the distributions of benthic invertebrates are aggregated (Elliot 1977).

The data from the Blane Water proved more difficult to analyse and interpret probably because of the more homogenous nature of the sampling points in this site. The range of depths was less than at the other sites and the substrate was always mainly gravel, see Chapter 2, Figures 2-7, 2-10. As the DCA examination showed the taxa appeared to follow a linear rather than a unimodal response to the environmental variables measured supporting the reasoning above.

Constraining ordinations with flow variables illuminated the individual taxon's preferences. Although the amount of variance explained by the direct gradient ordinations (CCAs) was low, suggested that the variables used are important influences on the spatial distribution of benthic invertebrates in Scottish rivers and elsewhere. A gradient between erosional and depositional conditions was displayed in both constrained ordinations along which some of the taxa exhibited preferences consistent with previously published data.

The small amount of variance in the species data explained by the ordination diagrams suggests that the variables selected are only one of many factors influencing the distribution of benthic invertebrates in the data set. That the multivariate environment of stream benthos is complex has frequently been recognised and its potential for limiting the success of such studies noted e.g. Williams & Smith (1996) endorses the sentiments of (Hart 1992):

"that meaningful models of lotic community structure will only arise if researchers acknowledge the multifactorial organisation and dynamic nature of these communities".

It has been pointed out previously that species abundance data are frequently very noisy leading to a small percentage of the variance in the data being explained (ter Braak & Smilauer 1998: p121). But it has also been stated that an ordination diagram that explains a low percentage of the data can be quite informative (Gauch 1982) e.g. the use of CA on benthic invertebrates data with comparable eigenvalues to the data presented here showed clear patterns in distribution in Italian river systems (Rossaro & Pietrangelo 1993).

There is another possible reason for the low amount of variance explained by the environmental variables, that is they were not measured on a physical or temporal scale suitable to easily detect invertebrate preferences. Downes has repeatedly shown that finer scale measurements of environmental variables yields illuminating results (Downes & Jordan 1993; Downes *et al.* 1995) as have others (Whetmore *et al.* 1990).

Unfortunately these papers have concentrated their fine scale measurements on larger substrate elements to the exclusion of other substrate types (sand, fine gravel) and therefore were not applicable here. Others have suggested that invertebrate distribution is a function of flow events that have preceded the current conditions (Clausen & Biggs 1997) or that conditions directly upstream can affect spatial distribution (Quinn *et al.* 1996). Although this is a persuasive argument, when one thinks of the disturbance caused by flooding it is not wholly convincing particularly in light of the rapid ability of invertebrates to recolonise the stream bed post disturbance (Brooks & Boulton 1991). This rapid response is somewhat dependent on the slope and bed structure of the river (Armitage & Gunn 1996). A final possibility is that different instars or species within a taxon had different habitat preferences but when amalgamated together under their taxon name these habitat preferences were hidden. It has been shown that small nymphs and large nymphs of *Ecdyonurus* species, a taxa occurring in this study exhibit preferences for different bed roughness (Buffagni *et al.* 1995).

There are many other possible reasons for the small amount of variation explained but they are not related to flow variables, e.g. predation or periphyton availability (Dudgeon & Chan 1992; Lancaster *et al.* 1990). It is not possible to discuss these factors in detail because no measurements of such interactions are recorded. Finally the possibility exists that the animals are not strongly influenced by the environmental variables measured.

That no additional variation in the data was explained by variables derived from velocity profiles was disappointing. Although others have successfully incorporated such measures into multivariate analysis of similar data (Quinn & Hickey 1994) I conclude that estimates of near-bed flow conditions derived from one velocity profile, measured over one spot on a river bed in a standard 25 x 25 cm quadrat are not applicable to the whole of that quadrat. The complex range of near-bed flow patterns that can occur in one quadrat would be the cause. The more traditional use of mean water column velocity and depth are more likely to be indicative of the incident flow arriving over a qaudrat and is applicable to the whole quadrat because it is not hugely effected by the bed form directly below. Measures of substrate type are important to complete the picture. The advent of new technology (acoustic doppler velocimeter) has allowed the rapid measurement of turbulence in 3 dimensions above the stream bed and has been shown as an important variable in the distribution of invertebrates (Bouckaert & Davis 1998). Although heeding the advice of Pringle *et al.* (1988): advise cited in the introduction (chapter 1) one imagines the incorporation of measures of turbulence into future sampling plans would be highly illuminating. Interestingly, test ordinations of the velocity profile variables showed the R^2 values for the profiles explained additional variation in the distribution of invertebrates (data not shown). As the R^2 value can be interpreted as a measure of the deviation of the flow structure above the bed from the a standard log-normal relationship it can be seen as a measure of gross turbulence (which would not be reflected in Re) and may provide a useful additional measure of habitat complexity.

3.5 Conclusions

- Unconstrained ordinations did not produce clear aggregations of taxa, mirroring some other studies.
- Constrained ordinations did show a gradient of erosional to depositional conditions with some taxa showing preferences for these conditions.
- Responses of some taxa varied between rivers as did the relationships between physical parameters measured, implying that models produced for one river are

likely to be site specific, limiting the use of IFIM based PHABSIM studies in river management of invertebrate habitat

- A re-evaluation of the importance of flow parameters is necessary with the inclusion of turbulence measurements, spatial scales tailored to individual species and more emphasis on alternative effects of flow parameters, e.g. spatial redistribution of invertebrates, conditions for periphyton growth etc.

Chapter 4: Individual responses to hydraulic parameters

4.1 Introduction

This chapter concentrates on the responses of individual taxa to the environmental variables measured in Chapter 2. The multivariate techniques used in Chapter 3 are based on the assumption that species respond to environmental gradients either in a linear or a unimodal manner. As the methods used are robust enough to deal with noisy data (Jongman *et al.* 1988) few users actually publish the underlying response curves of the species of interest. This pragmatic approach has left significant gaps in our knowledge. As mentioned in the previous chapter, management tools such as PHABSIM make a number of assumptions about the responses of animals, including a constant or fixed response curve to flow (Milhous *et al.* 1984).

Finding information to support these assumptions is very difficult simply because there is such a small amount of published data on species responses to individual flow variables. Only three references were found (Jowett *et al* 1991; Lancaster1999; Fjellheim 1996) which give response plots of invertebrates to flow variables in the field using measures of abundance. Based on presence absence data others have provided logistic (or logit) regression analysis curves, plotting the probability of gammarid species occurring along various environmental gradients (Peeters & Gardeniers 1998) including water velocity. The technique has also been successfully applied to the distribution of water beetles, although the interest here, was mainly in lentic species (Eyre *et al.* 1992; Eyre *et al.* 1993).

There have been a large number of papers examining the flow preferences of freshwater benthic invertebrates in the field. Some older studies do look at individual variables but the results tend to be descriptive only (Jones *et al.* 1977). Of the more recent works few look at variables singly instead, analysis tends to be multivariate

(Downes *et al.* 1995; Hawkins *et al.* 1997; Puckridge *et al.* 1998). This makes sense when one is dealing with a large number of variables and species, especially as many of the variables may have synergistic effects. However examination of responses of individual species or taxa allow us to ask some important questions.

The first question is whether or not the animals actually respond to the variables at all and if they do, do they conform to our views of niche occupation. In attempts to show taxon preferences, abundance can be plotted against an environmental variable and a curve fitted.

If the environmental variable data was collected using a randomised sampling regime any curve fitted to the data is highly dependent on the distribution of the environmental variable. For example a taxon may prefer a velocity of 0.5 ms^{-1} but 0.2 ms^{-1} is the most common velocity sampled and lies within the taxon's velocity tolerance range. Then the taxon's maximum abundance could occur at 0.2 ms^{-1}. A fitted curve describing this type of response represents the taxon's compromise distribution.

Data collected in this manner has been used to produce in-stream flow-habitat suitability curves for benthic invertebrates (Jowett *et al.* 1991). So the possibility exists that the invertebrate's actual preferences are not being identified and the models are based on incorrect assumptions. This is more likely to happen if the species have a broad tolerance for the environmental variables in question and also covers the available range of the environmental variable. Unfortunately these studies do not report the distribution of the environmental variables of interest so it is impossible to judge the quality of their results.

Here abundance of individual taxa is plotted against depth, velocity and substrate type with frequency histograms of these environmental variables also present. The relationship between the environmental variables and taxon abundance was tested in two ways for each taxon.

Where possible the following hypotheses were tested:

H'_o: That the animals were responding to individual flow variables in a gaussian manner, this response includes both linear and unimiodal response types.

H^2_o:That the observed responses were not artifacts of the sampling program and did indicate an actual response by the invertebrates.

It was not possible to test the second hypothesis conclusively. But it was believed that if the maximum abundance of a taxon in individual samples (dependent variable) was correlated to the uneven sampling of the environmental (independent) variable that this might indicate any relationship was a sampling artifact.

By this I mean that variables such as velocity, if recorded at random sampling points in a stream will show a strongly schewed distribution, e.g. some velocities are being recorded more frequently, their 'abundance' is higher. If velocity does not have a large influence on the distribution of a particular species it may still show a positive correlation with the more common velocities simply because these represent more frequently sampled points on the river bed and with each sample ones chances of recording the animals at high densities increases. Therefore I predict that a given taxon will reach its maximum abundance in samples in which the environmental variable also reaches its maximum abundance e.g. if the most frequent velocity was 0.25 ms^{-1} then the species of interest would reach its maximum abundance in areas of the river where that velocity occurred.

To ecologists there is an obvious alternative reason why a species would occur at the most frequently available point along an environmental gradient and that is because it is highly adapted to it! However some of the variables measured, such as depth and velocity alter on a daily or even hourly basis in rivers so it would be odd that the animals were exactly adapted to the conditions on the day, but not on the previous day for example. It was not possible to exclude this possibility from the analysis but it is hoped that by presenting the responses of the animals at each site separately, comparisons of responses at the different rivers would aid the evaluation of this possibility.

4.2 Methods

4.2.1 Data

The data collection methods are given in Section 2.2 of Chapter 2. Not all taxa sampled were used in model fitting. Those excluded had low occurrences. The samples taken were quantitative and are represented as numbers of individuals per sample in all cases. Actual number of animals recorded is used in the response plots, so the reader can clearly see the number of individuals each plot is based upon.

4.2.2 Statistical Analysis

To test the two hypotheses each environmental variable was divided into a number of intervals and the frequency of each interval calculated (frequency = no. of samples in which that interval occurred). The intervals for each variable, at the three rivers are given in tables 4-1, 4-2 and 4-3. Intervals were chosen using a pragmatic approach which attempted to assign the same number of intervals to the same variable at all sites, which was not always possible due to the distribution of the variables. It is possible that by increasing the number of intervals I increased n and the possibility of getting a significant correlation but if I had given the same number of intervals to all variables their occurrence would have been too low in all categories to show any responses. **The maximum sample abundance** of each taxon for each interval was identified using an excel pivot table. By maximum sample abundance for a particular interval I mean the density of individuals occurring within a sample which has the highest density of individuals for all samples whose environmental variable measures fall within that interval. Least squares regression was performed with the frequency of a given variable's intervals as the independent variable and the maximum density of individuals per interval as the response variable. This analysis was repeated for each taxon at each river. The results of this analysis are presented in a general review of taxon responses to environmental variables which also includes non - significant responses. The **totalled abundances** were also examined to test the second hypothesis and represent the summed abundance for a particular interval.

Table 4-1, Velocity (mean water column velocity) intervals used in regression analysis.

R. Etive		Duneaton Water		Blane Water	
Intervals ms^{-1}	Frequency	Intervals ms^{-1}	Frequency	Intervals ms^{-1}	Frequency
0-0.05	7	0-0.05	14	0-0.1	6
0.05 - 0.1	8	0.05 - 0.1	4	0.1 - 0.2	4
0.1-0.15	7	0.1-0.15	6	0.2-0.3	4
0.15 - 0.2	6	0.15 - 0.2	5	0.3 - 0.4	10
0.2 - 0.25	2	0.2 - 0.25	6	0.4 - 0.5	2
0.25 - 0.3	5	0.25 - 0.3	1	0.5 - 0.6	4
0.3 - 0.35	2	0.3 - 0.35	6	0.6 - 0.7	4
0.35 - 0.4	2	0.35 - 0.4	1	0.7 - 0.8	1
0.4 - 0.45	3	0.4 - 0.45	2	0.8 - 0.9	1
0.55 - 0.6	2	0.5 - 0.55	1	0.9-1.0	2
0.6 - 0.65	2	0.55 - 0.6	1	>1.0	2
0.65 - 0.7	3	0.6 - 0.65	2		x
>0.7	2	0.65 - 0.7	2		x

Table 4-2, Depth intervals used in regression analysis.

R. Etive Interval m	Frequency	Duneaton Water Interval m	Frequency	Blane Water Interval m	Frequency
0-0.05	3	0-0.05	6	0-0.05	6
0.05 - 0.1	3	0.05 - 0.1	9	0.05 - 0.1	11
0.1-0.15	6	0.1-0.15	8	0.1-0.15	6
0.15 - 0.2	10	0.15 - 0.2	7	0.15 - 0.2	7
0.2 - 0.25	7	0.2 - 0.25	9	0.2 - 0.25	6
0.25 - 0.3	3	0.25 - 0.3	4	0.25 - 0.3	1
0.3 - 0.35	4	0.3 - 0.35	3	0.3 - 0.35	2
0.35 - 0.4	4	0.35 - 0.4	3	>0.5	1
0.4 - 0.45	1	0.4 - 0.45	3		
0.5 - 0.55	4	0.45-0.5	1		
0.55 - 0.6	1				
0.6 - 0.65	1				
0.65 - 0.7	1				
>0.7	3				

Table 4-3, Substrate intervals used in regression analysis. Percentage composition of standard substrate units, cobble, gravel etc., were transformed to average length measures in mm by taking the mean length of each substrate category and using it to get the weighted average for each sample.

R. Etive		Duneaton Water		Blane Water	
Interval mm	Frequency	Interval mm	Frequency	Interval mm	Frequency
0-50	11	0-20	12	0-10	1
50-100	11	20-40	13	10-20	2
100-150	4	40-60	6	20-30	7
100-200	5	60-80	5	30-40	12
200-250	7	80-100	9	40-50	10
250-300	12	100-120	1	50-60	1
		>120	7	>60	5

I attempted to fit Gaussian curves to the abundance data directly using a version of the method suggested by (Jongman *et al.* 1987): c.f. Section 3.4 'Regression for abundance data with many zero values'. They advocate the use of log-linear regression where the Gaussian curve takes the form:

$$log(y) = b_0 + b_1x + b_2 x^2$$

where $b_2 < 0$. As the term $b_0 + b_1x + b_2 x^2$ is a linear predictor it allows the use of multiple regression applications in statistical packages where x and x^2 can be entered as separate variables (Lancaster, J. Edinburgh University pers comm.). This was the method used here. There is an alternative form of the equation which has some attraction for biologists this is:

$$log(y) = a - 0.5(x - u)^2 / t^2$$

such that u is the optimum position of the species along the environmental gradient (value of x where the maximum abundance occurs), t is its tolerance (a measure of ecological amplitude) and a is the log of the species maximum abundance (c) (ter Braak & Prentice 1988).

It is possible to estimate these parameters using the following conversions:

the optimum, $u = - b_1/(2b_2)$

the tolerance, $t = 1 / \sqrt{(-2b_2})$

the maximum, $c = exp(b_0 + b_1x + b_2 x^2)$

4.3 Results

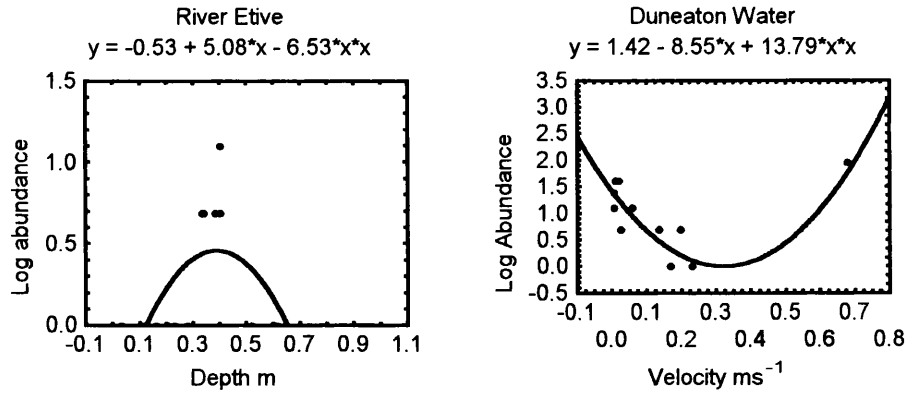
The results are divided into three main sections; one for each environmental variable. These sections are subdivided by river and at the end of each section, comments on taxa which occur in more than a single river are made. Presentation of information as basic scatter plots of individual taxa against environmental variables aids interpretation of the statistical analyses. An introductory review of these analyses is followed by the presentation of the results by variable and by taxon.

4.3.1 Curve Fitting

Attempts to fit Gaussian curves to the data produced mainly non-significant results, in spite of the apparent unimodal responses suggested by many of the scatter plots of abundance against environmental gradients, see Appendix V. Of the cases where curves fitted were significant see Figure 4-1.

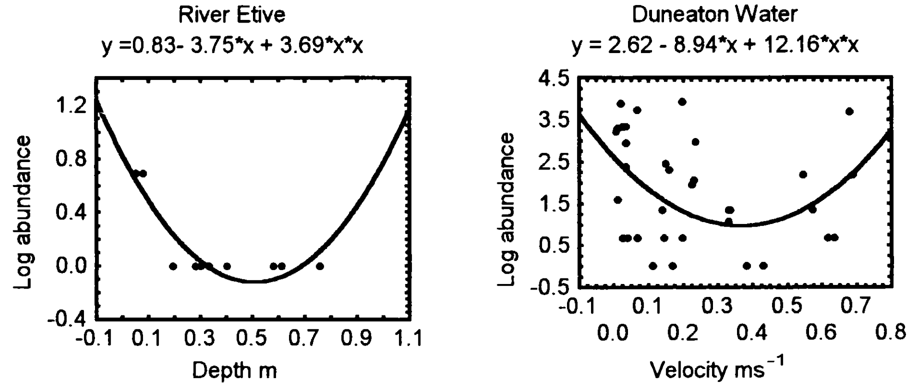
4.3.2 Relationships of totalled maximum abundance to the frequency of variable intervals

For the majority of taxa which did show a significant response, the correlations were moderate; for 26 out of the 31 significant correlation's, the R^2_{adj} value was less than 0.75, figs 4-2a, 4-2b, and 4-3. Of the 3 variables examined, substrate had the fewest significant correlations (6), all of which were for the Blane Water. Depth intervals were most frequently correlated (14) and velocity intervals were the second most



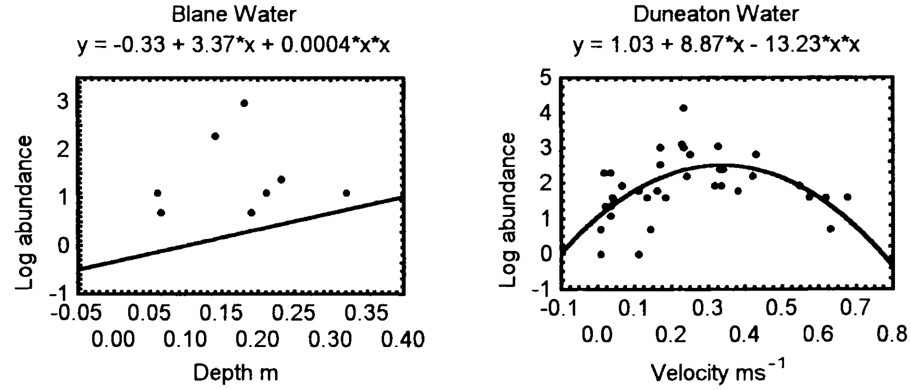
Tanypodinae

Oulimnius tuberculatus



Polycentropus flavomaculatus

Chironomidae



Ancylus fluviatilis

Ecdyonurus spp

Figure 4-1. Plots of log abundance against depth or velocity for animals exhibiting statistically significant gaussian relationships.

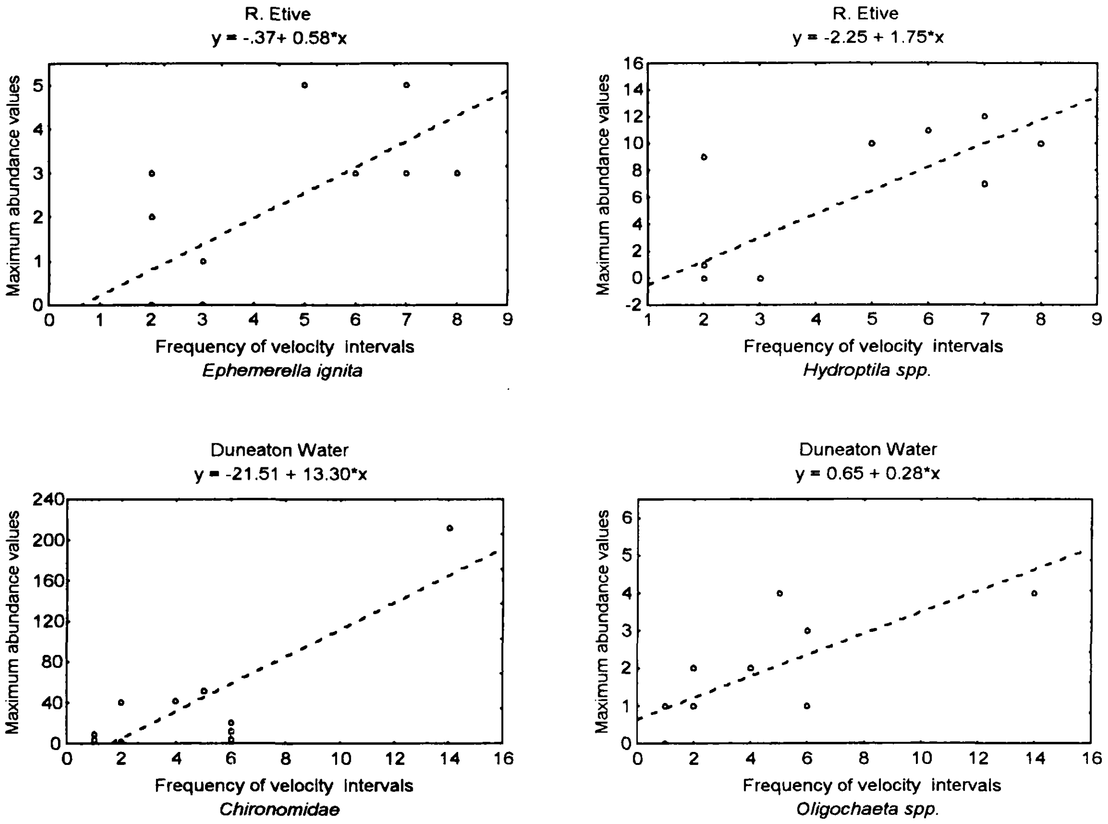


Figure 4-2a, Regression scatter plots of maximum sample abundance against frequency of velocity intervals. *Ephemerella ignita*, $p < 0.01$, $R^2_{adj} = 0.47$ $F = 11.73$, $n = 13$; *Hydroptila spp.*, $p < 0.01$, $R^2_{adj} = 0.58$, $F = 18.10$, $n = 13$; Chironomidae, $p < 0.001$, $R^2_{adj} = 0.69$, $F = 28.9$, $n = 14$ and Oligochaeta spp., $p < 0.01$, $R^2_{adj} = 0.54$, $F = 15.41$, $n = 14$.

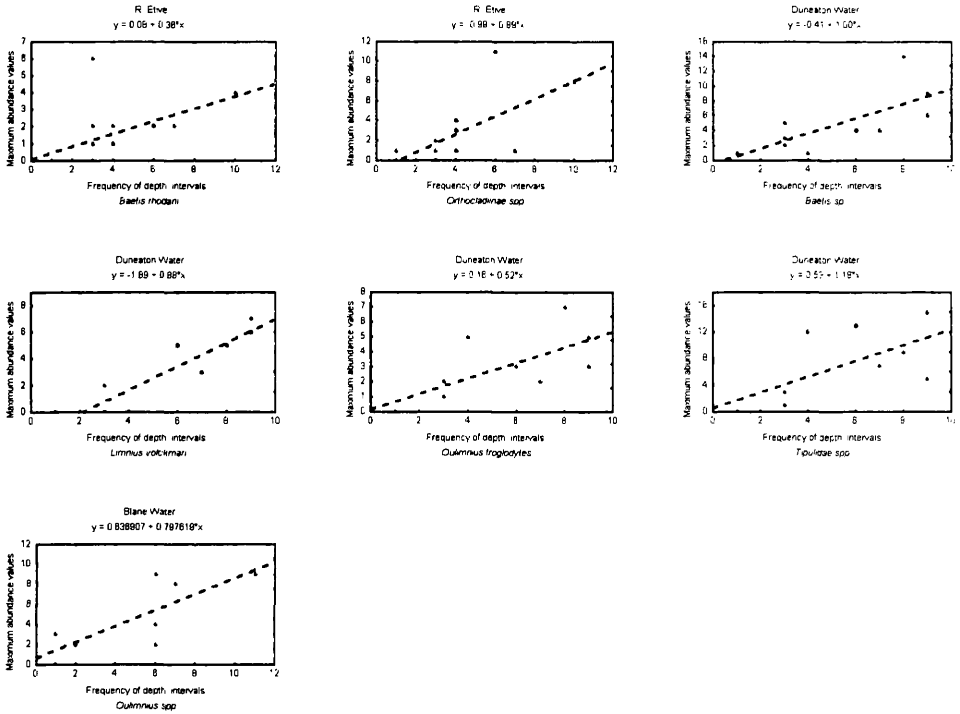


Figure 4-2b, Regression scatter plots of maximum sample abundance against frequency of depth intervals. Orthocladiinae spp. $p < 0.01$, $R^2_{adj} = 0.44$ F =11.38, n = 14; *Baetis rhodani* $p < 0.05$, $R^2_{adj} = 0.286$ F = 4.8, n = 14; *Baetis* spp. $p < 0.05$, $R^2_{adj} = 0.45$, F = 8.46, n = 10; *Limnius volckmari* $p < 0.001$, $R^2_{adj} = 0.81$, F = 40.31, n = 10; *Oulimnius troglodytes* $p < 0.05$, $R^2_{adj} = 0.39$, F = 6.85, n = 10; Tipulidae. $p < 0.05$, $R^2_{adj} = 0.34$, F =5.67, n = 10 and *Oulimnius* spp. $p < 0.05$, $R^2_{adj} = 0.54$, F = 9.31, n = 8.

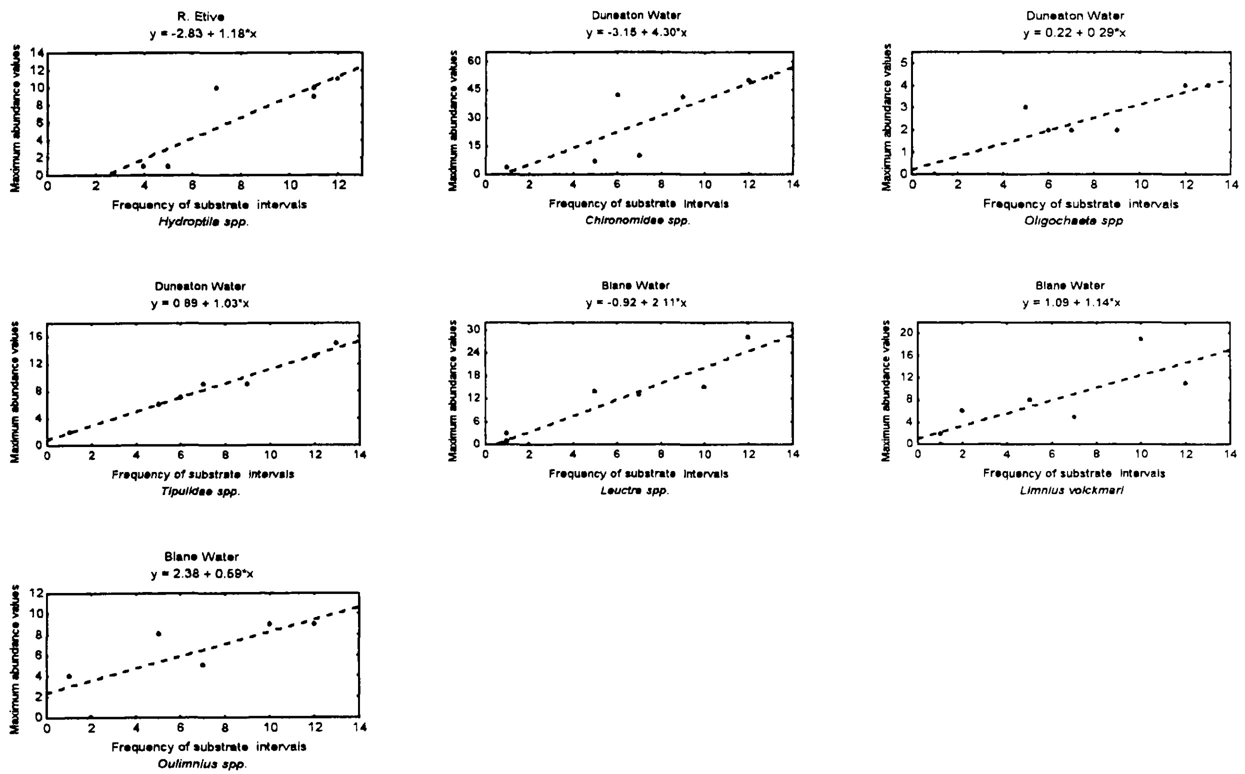


Figure 4-3, Regression scatter plots of maximum sample abundance against frequency of substrate intervals. *Hydroptila spp.* $p < 0.05$, $R^2_{adj} = 0.68$, F =12.04, n = 6; Chironomidae spp. $p < 0.05$, $R^2_{adj} = 0.63$, F =11.55, n =7;Oligochaeta spp. $p < 0.05$, $R^2_{adj} = 0.70$, F =15.40, n =7; Tipulidae spp. $p < 0.0001$, $R^2_{adj} = 0.97$, F =201.0, n = 7; Leuctra spp. $p < 0.01$, $R^2_{adj} = 0.85$ F = 35.77, n = 7; *Limnius volckmari* $p < 0.05$, $R^2_{adj} = 0.57$ F = 8.82, n = 7; *Oulimnius spp.* $p < 0.05$, $R^2_{adj} = 0.54$, F = 8.18, n = 7.

frequently correlated (11). The R. Etive had the fewest significant conditions, reflecting the limited number of taxa which occurred in sufficient abundance to be assessed. The Duneaton Water had fewer significant relationships than the Blane Water.

4.3.3 Relationships between maximum sample abundance to the frequency of variable intervals

Significant relationships were limited to a small number of the taxa. With the exception of substrate, which had 7 significant correlations, the number of correlations was fewer than for the relationships between totalled abundance and the environmental variables depth (7) and velocity (4): Table 4-4.

There were no significant correlations for velocity at the Blane Water which was represented among the sites with significant relationships for the other two variables. It had the fewest significant relationships of all sites with 4 in total while the R. Etive had 5 and the Duneaton Water had 9.

Table 4-4, The results of the regression analysis of totalled taxa abundances (dependent variable) against frequency of environmental gradient intervals (independent).

Variable	River	Taxon	p value	F statistic	R^2_{adj}	n	bo	b1
Velocity	R. Etive	*Ephemerella ignita*	<0.01	(1,11) 11.42	0.46	13	-0.8	0.97
		Hydroptila	<0.0001	(1,11) 56.98	0.82	13	-6.76	3.82
		Tanypodinae	<0.01	(1,11) 14.42	0.52	13	-0.706	0.611
		Tipulidae	<0.001	(1,11) 31.06	0.71	13	-1.22	0.68
	Duneaton Water	Chironomidae	<0.001	(1,11) 32.68	0.73	13	-52.25	25.94
		Oligochaeta	<0.0001	(1,11) 99.8	0.89	13	-1.05	1.17
		Oulimnius troglodytes	<0.001	(1,11) 20.09	0.614	13	-1.88	1.16
		Tipulidae	<0.05	(1,11) 6.15	0.3	13	5.5	1.26
	Blane Water	*Ephemerella ignita*	<0.05	(1,9) 8.84	0.43	11	18.09	23.09
		Ecdyonurus	<0.05	(1,9)6.31	0.347	11	3.27	2.64
		Oulimnius	<0.01	(1,9) 12.41	0.53	11	-1.21	2.4
		Leuctra	<0.01	(1,9) 10.43	0.48	11	-2.93	5.2
Depth	R. Etive	*Baetis rhodani*	<0.01	(1,12) 9.99	0.4	14	-0.93	0.96
		Orthocladiinae	<0.001	(1,12) 19.61	0.58	14	-2.84	1.77
		Tipulidae	<0.05	(1,12) 6.11	0.228	14	0.36	0.27
	Duneaton Water	Chironomidae	<0.05	(1,5) 11.14	0.62	7	-23.46	11.47
		Ephemerella ignita	<0.01	(1,9) 15.22	0.58	11	24.75	0.78
		Oligochaeta	<0.05	(1,5) 9.15	0.57	7	-0.37	2.93
		Oulimnius tuberculatus	<0.05	(1,9) 8.38	0.42	11	30.86	..72

Variable	River	Taxon	p value	F statistic	R^2_{adj}	n	bo	b1
		Tipulidae	<0.05	(1,5) 9.15	0.57	7	-0.37	2.93
	Blane Water	*Ecdyonurus*	< 0.05	(1,6) 11.28	0.594	8	-1	3.75
		Elmis aenea	<0.005	(1,6) 18.73	0.716	8	-2.6	2.09
		Ephemerella ignita	<0.05	(1,6) 6.47	0.43	8	14.77	25.11
		Limnius volckmari	<0.05	(1,6) 7.65	0.48	8	-1.23	3.04
		Leuctra	<0.05	(1,6) 8.28	0.51	8	2.17	3.96
		Oulimnius	<0.005	(1,6) 19.02	0.72	8	-2.72	2.61
	Blane Water	*Baetis rhodani*	<0.01	(1,5) 20.44	0.76	7	-2.46	2.08
Substrate		*Ephemerella ignita*	<0.005	(1,5) 25.61	0.8	7	-16.1	30.2
		Leuctra sp.	<0.005	(1,5) 33.45	0.84	7	-8.48	6.01
		Limnius volckmari	<0.05	(1,5) 11.59	0.63	7	-3.18	3.42
		Oulimnius sp.	<0.005	(1,5) 37.42	0.85	7	-1.42	2.41

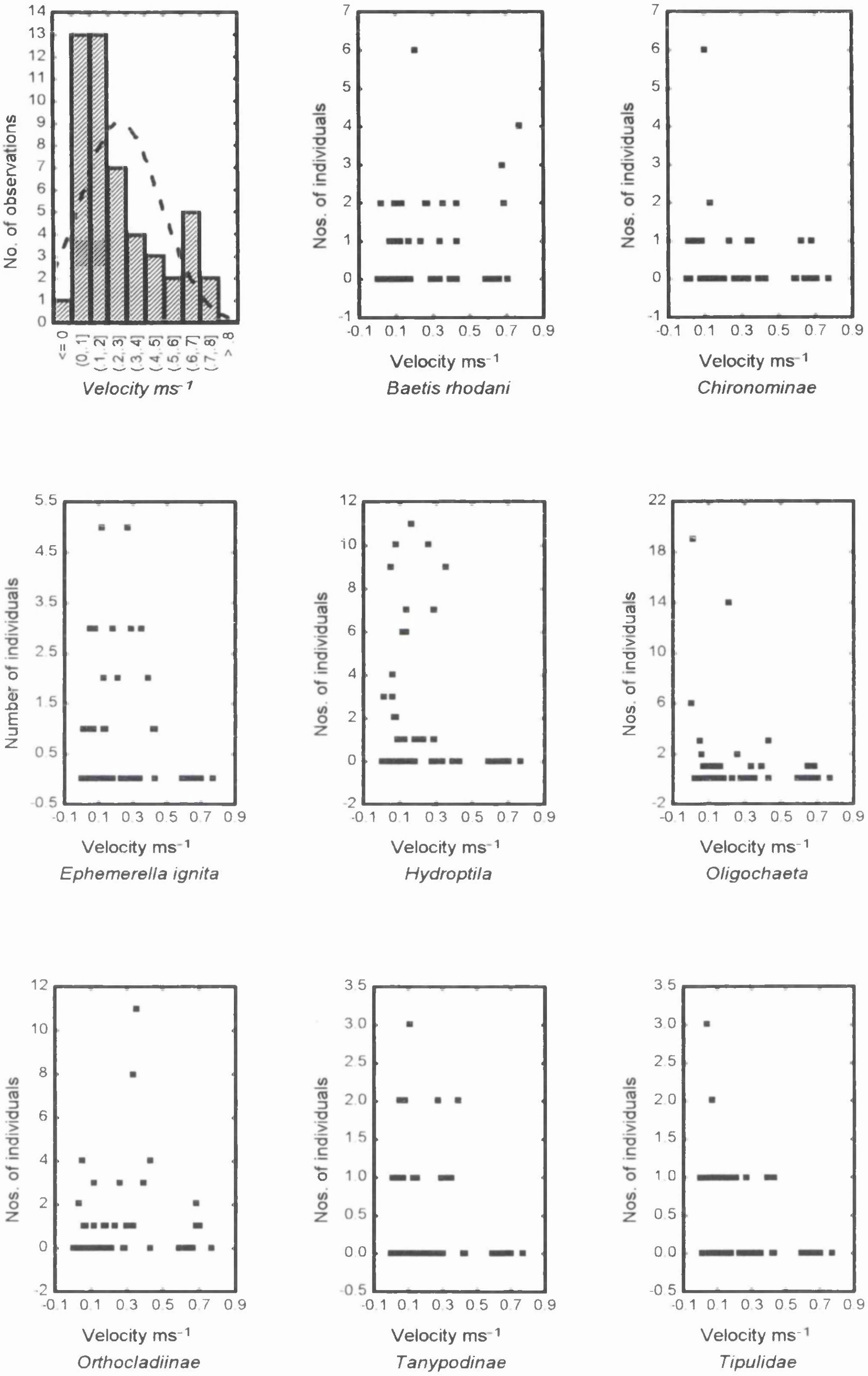
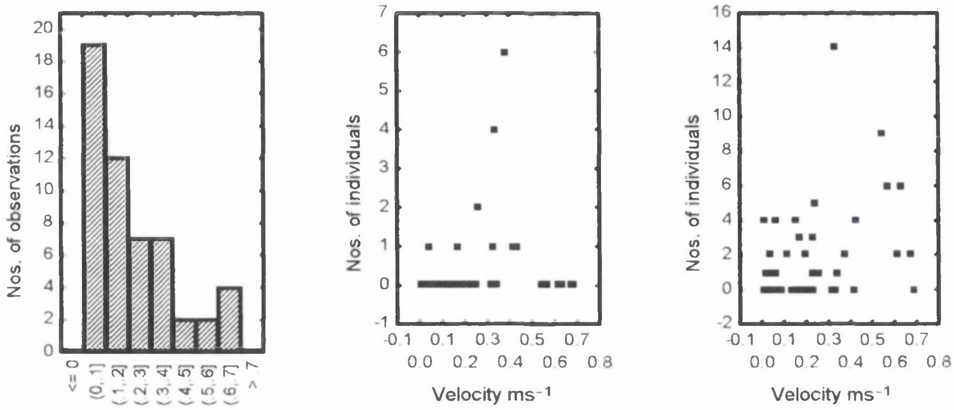
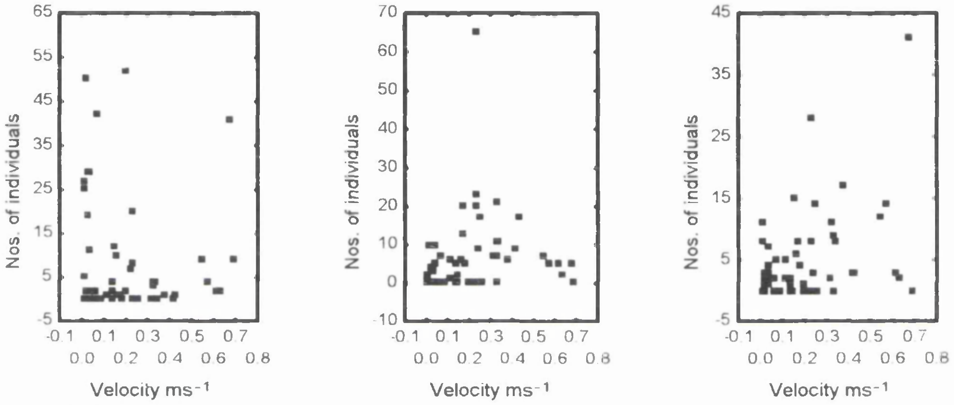


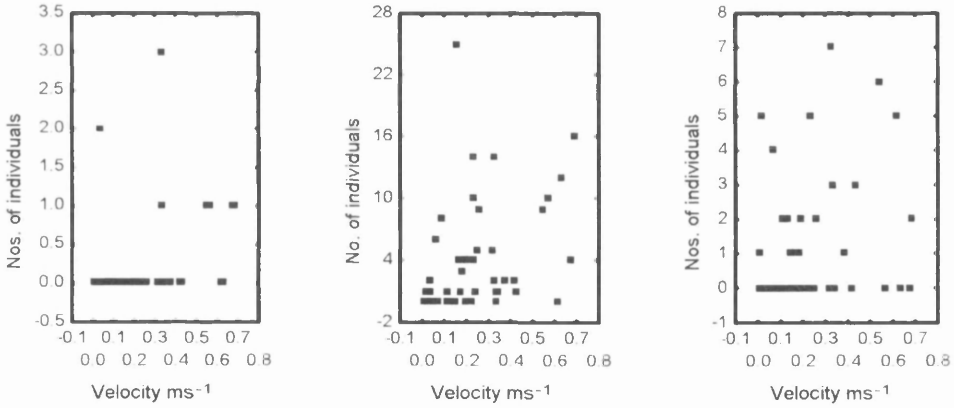
Figure 4-4, Etive velocity scatter plots with a histogram showing the frequency distribution of velocity at sampling points. Abundance values are number of individuals per sample.



Velocity ms^{-1} *Ancylus fluviatilis* *Baetis sp.*

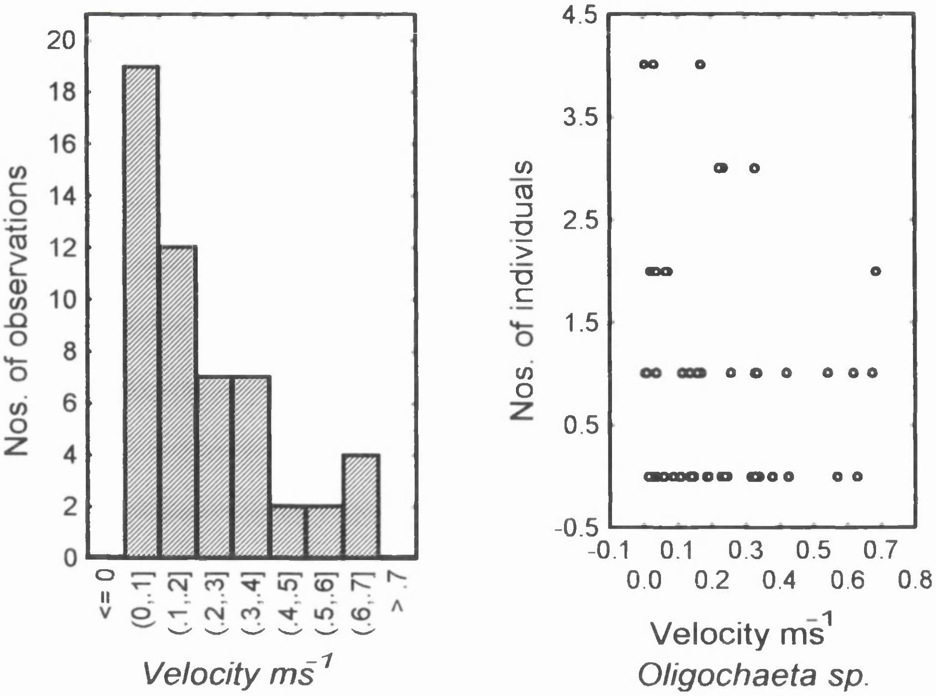


Chironomidae spp. *Ecdyonurus spp.* *Ephemerella ignita*

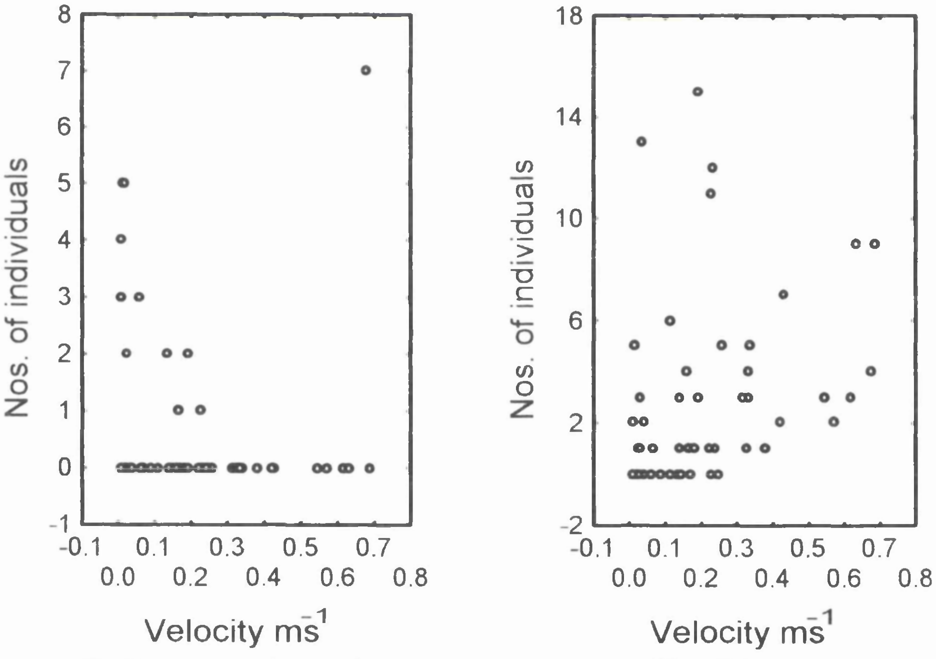


Hydropsyche sp. *Leuctra spp.* *Limnius volckmari*

Figure 4-5a, Duneaton Water velocity scatter plots with a histogram showing the frequency distribution of velocity at sampling points. Abundance values are number of individuals per sample.



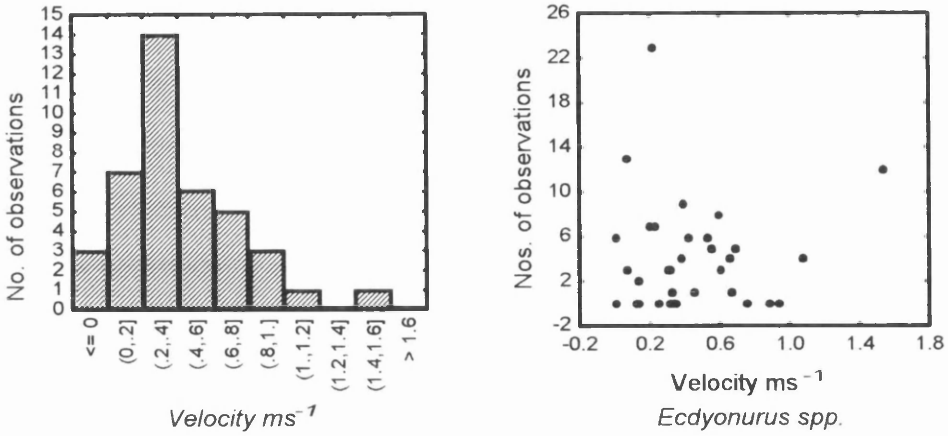
Oligochaeta sp.



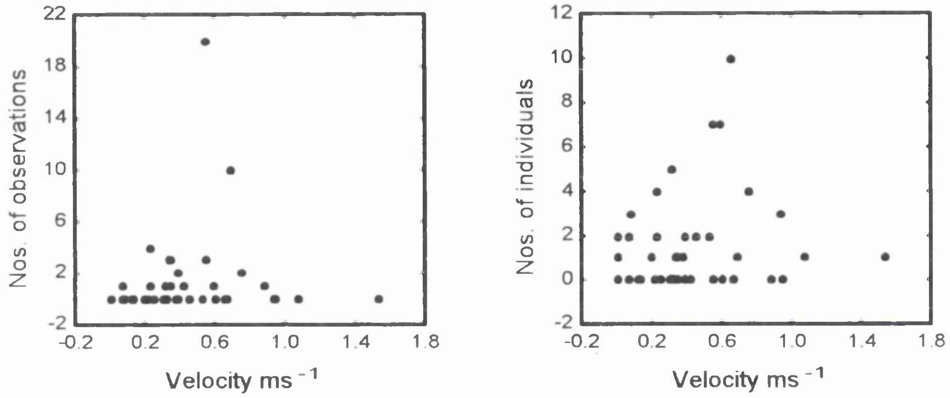
Oulimnius tuberculatus

Tipulidae spp.

Figure 4-5b, Duneaton Water velocity scatter plots with a histogram showing the frequency distribution of velocity at sampling points. Abundance values are number of individuals per sample.

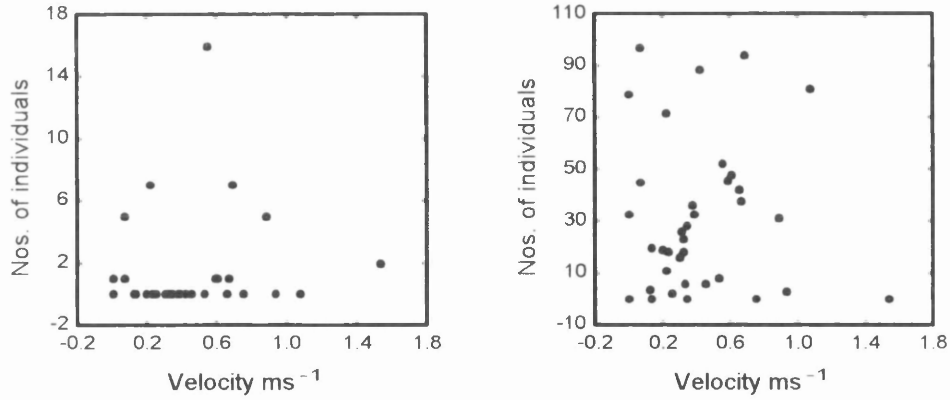


Ecdyonurus spp.



Ancylus fluviatilis

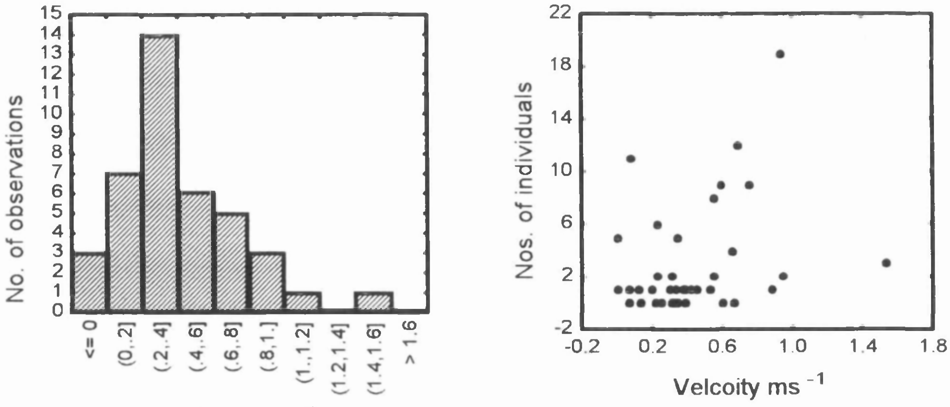
Elmis aenea



Baetis rhodani

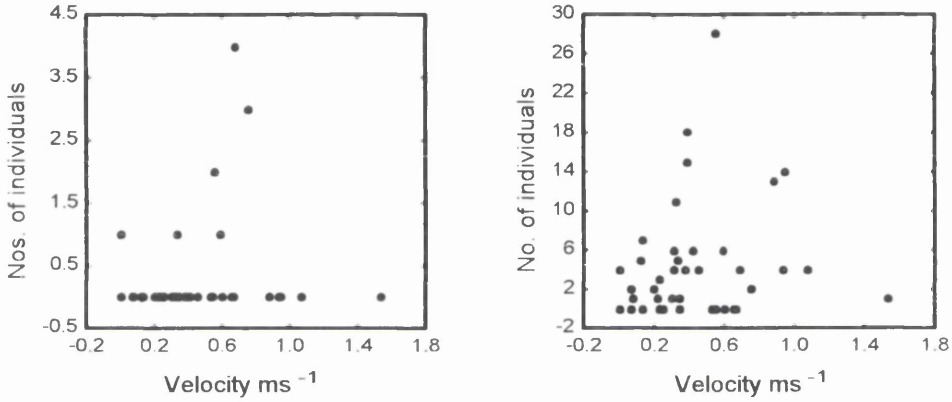
Ephemerella ignita

Figure 4-6a, Blane Water velocity scatter plots with a histogram showing the frequency distribution of velocity at sampling points. Abundance values are number of individuals per sample.



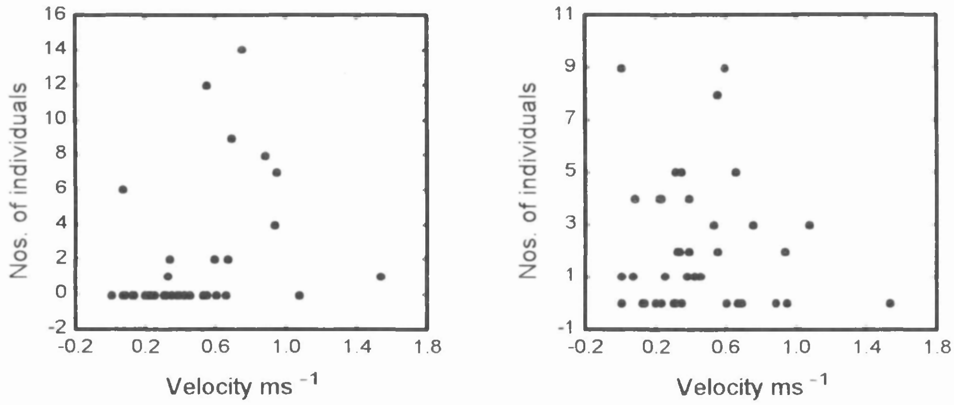
Velocity ms^{-1}

Limnius volckmari



Agapetus fuscipes

Leuctra spp.



Glossoma boltoni

Oulimnius spp.

Figure 4-6b, Blane Water velocity scatter plots with a histogram showing the frequency distribution of velocity at sampling points. Abundance values are number of individuals per sample.

4.3.4 Velocity

River Etive

The majority of the taxa (6 out of 8) assessed were most abundant in samples where velocity was 0 - 0.2ms^{-1}, the most frequent velocity class, Fig 4-4. Of these Oligochaeta, *Tanypodinae* and Tipulidae showed a decreasing maximum sample abundance which is coincident with a decrease in occurrence of velocity, Fig 4-1. The totalled abundance of *Hydroptila* spp., Tanypodinae, Tipulidae and *E. ignita* were also significantly correlated with the frequency intervals, Table 4-2. *Baetis rhodani*, *Hydroptila* spp. and *Ephemerella ignita* appear to have a broader tolerance than the other three taxa, occurring in relatively high numbers up to 0.5ms^{-1} or 0.7ms^{-1} in the case of *B. rhodani*, Fig 4-4. The *Orthocladiinae* show maximum abundance in samples of higher velocity 0.3-0.4 ms^{-1}. Of all the taxa, *Ephemerella ignita* and the *Hydroptila* spp. were the only taxa which have their maximal abundance correlated to frequency of velocity intervals.

Duneaton Water

The frequency distribution of velocity at the Duneaton Water was log-normal and similar to that at the R. Etive, Fig 4-5a, b. Few taxa exhibit the same pattern of maximum sample abundance coincident with the commonest velocity observed at the R. Etive. Only the maximum sample abundance of the Oligochaeta and Chironomidae showed a significant correlation with the frequency of velocity intervals, Fig 4-1. The totalled abundance of both these taxa were also significantly correlated with velocity intervals, as are those of the Tipulidae and *Oulimnius troglodytes*, Table 4-4.

The maximum for *E. ignita* was near 0.25 ms^{-1} (excluding the outlier at 0.7 ms^{-1}) somewhat higher than at the R. Etive although it again exhibited a wide tolerance. *Baetis sp. Ancylus fluviatilis, Hydropsyche* sp. and *Limnius volckmari* all have a maximum abundance between 0.3 - 0.4 ms^{-1} which was higher than that at the most abundant velocities. *L. volckmari* also appeared to have a wide tolerance. The remaining taxon, *Ecdyonurus* spp. had its highest abundance at 0.2 ms^{-1}.

Blane Water

The distribution of velocity is unimodal, skewed to the right and different from the other two rivers, Fig 4-6 a,b. The most abundant velocity here was higher than at the other two sites being between 0.2 and 0.4 ms^{-1}. Here only *Ecdyonurus* spp. appeared to follow the distribution of velocities but, like all other taxa at the site, its maximum sample abundance did not show a statistically significant correlation with frequency of velocity. Its totalled abundance was significantly correlated with depth intervals as was that of *E. ignita, Oulimnius* and *Leuctra* spp, Table 4-4.

The most frequent velocity interval was around 0.6 - 0.7 ms^{-1}. The majority of the taxa appeared to have their maximum sample abundance at slightly higher velocities than this interval; included in this list are *Elmis aenea, Glossoma boltoni, Leuctra* spp., *Oulimnius* spp. *Agapetus fuscipes, Ancylus fluviatilis* and *Baetis rhodani,* Fig 4-6 a,b. *L. volckmari* had an even higher maximum sample abundance at 1.0 ms^{-1}.

Cross site comparisons

Taxa occurring at all sites

E.ignita

At the Blane Water and the Duneaton Water, *E.ignita* occurred in high numbers in samples at all available velocities. At the R. Etive there was a sharp decrease in occurrence around 0.5 ms^{-1}. . At the other two sites where it was more abundant, it occurs at higher velocities, 0.7 ms^{-1} in the Duneaton Water and 1 ms^{-1} in the Blane Water. The low abundance at these velocities in the R. Etive would appear to be a function of the very low abundance of *E. ignita* in the upland river as opposed to reflecting any particular velocity preference.

So although significant correlations between maximum sample abundance of *E. ignita* and velocity were recorded for the R. Etive data, the response to velocity should be viewed cautiously. The Blane Water had the widest range of velocities and high abundances of the animal and should give a truer reflection of the animals preferences. Here the totalled abundance of animals was only correlated with velocity intervals.

Baetis spp.

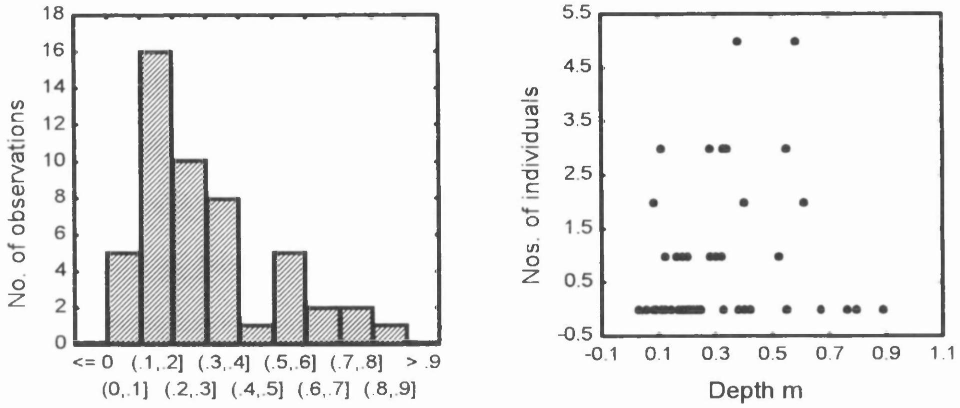
At both the Duneaton and Blane the taxon showed maximum abundance in samples with velocities just higher (0.4 and 0.5 ms^{-1} respectively) than the most available velocities; 0.1-0.2 ms^{-1} and 0.2-0.4 ms^{-1} respectively. It was not correlated with velocity in any of the rivers.

Taxa occurring in the R. Etive and Duneaton Water

At both sites the Chironomidae showed a preference for low velocities although there is one outlier at 0.7 ms^{-1} at the Duneaton Water. At both sites, totalled abundance was significantly correlated with depth intervals as was sample maximum at the Duneaton Water. Abundance of Oligochaeta at both sites was low and decreased with increasing velocity in a linear manner. At the Duneaton Water it showed significant relationships with available velocity intervals. The Tipulidae exhibited a wide tolerance for all velocities encountered.

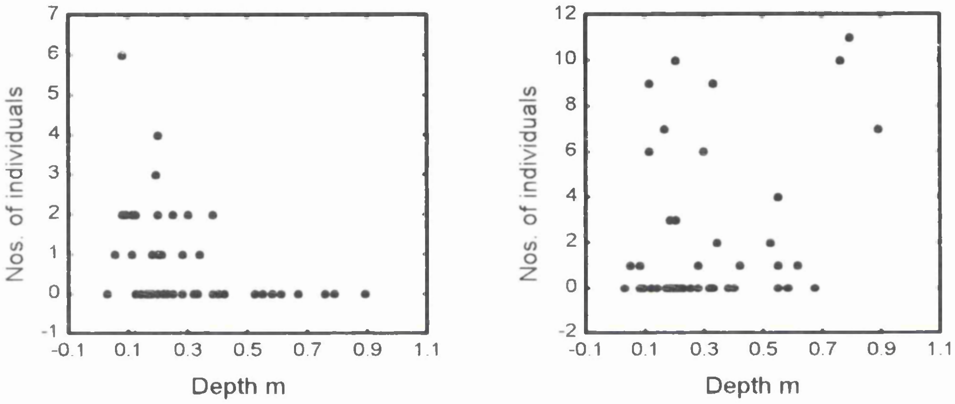
Taxa occurring in the Duneaton Water and Blane Water

Leuctra spp. occurred at high abundances across all velocities with the animal exhibiting a wider range in the Blane.



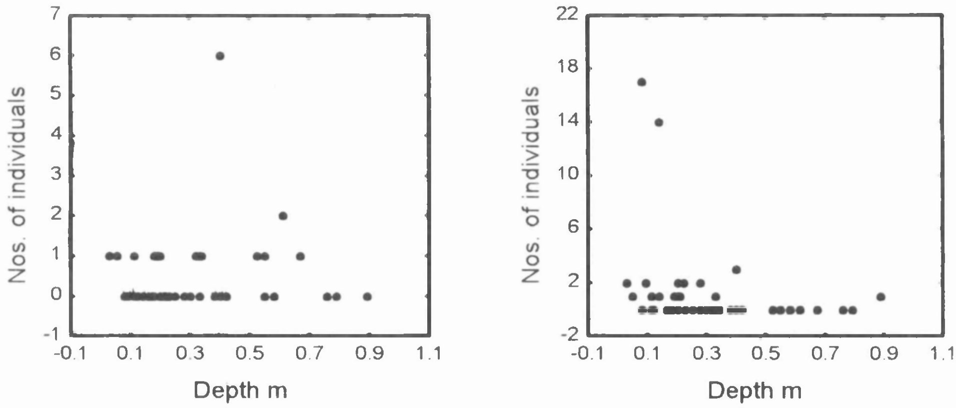
Depth m

Ephemerella ignita



Baetis rhodani

Hydroptila



Chironominae

Limnius volckmari

Figure 4-7a, River Etive depth scatter plots with a histogram showing the frequency distribution of depth at sampling points. Abundance values are number of individuals per sample.

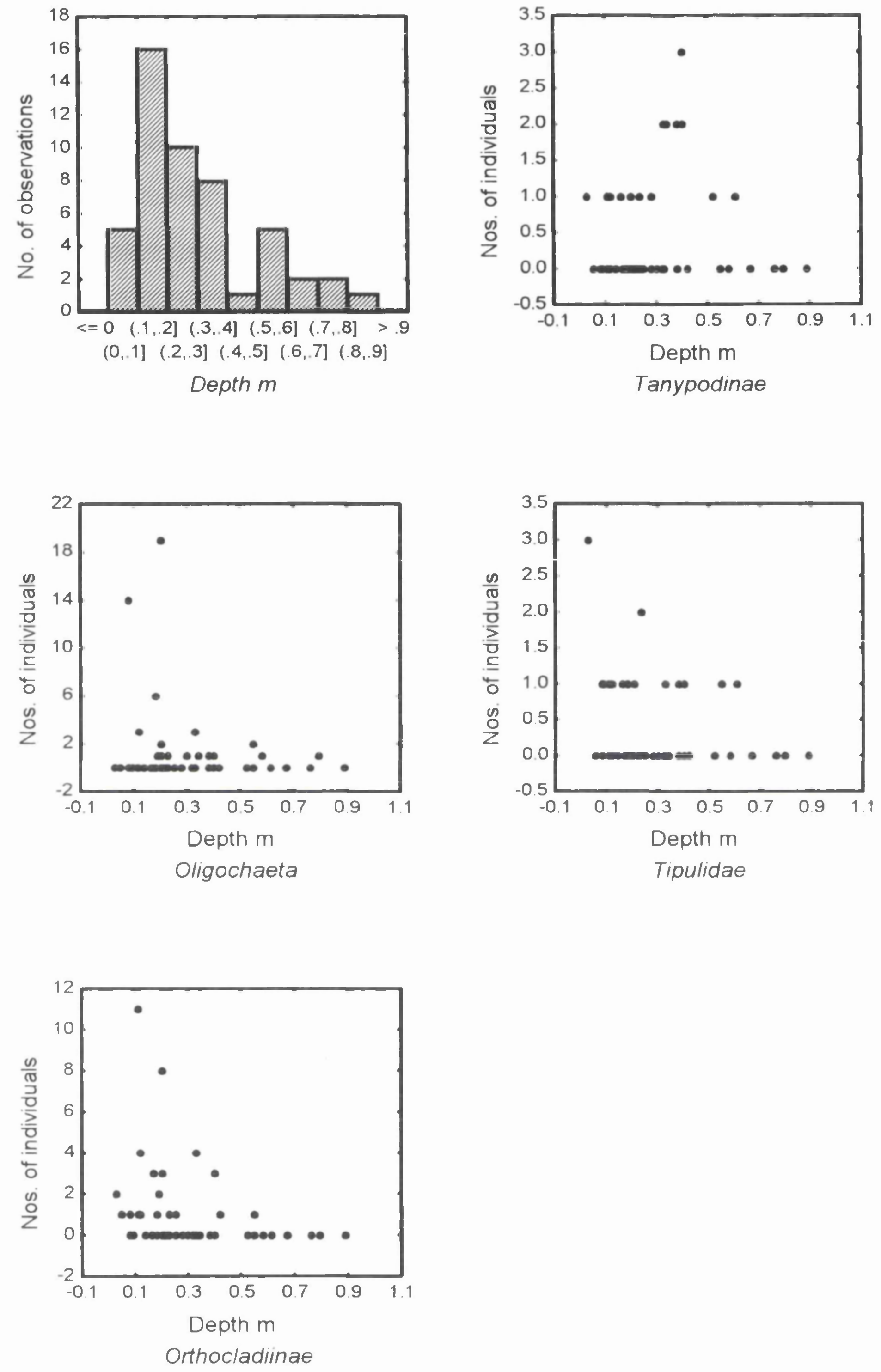


Figure 4-7b, River Etive depth scatter plots with a histogram showing the frequency distribution of depth at sampling points. Abundance values are number of individuals per sample.

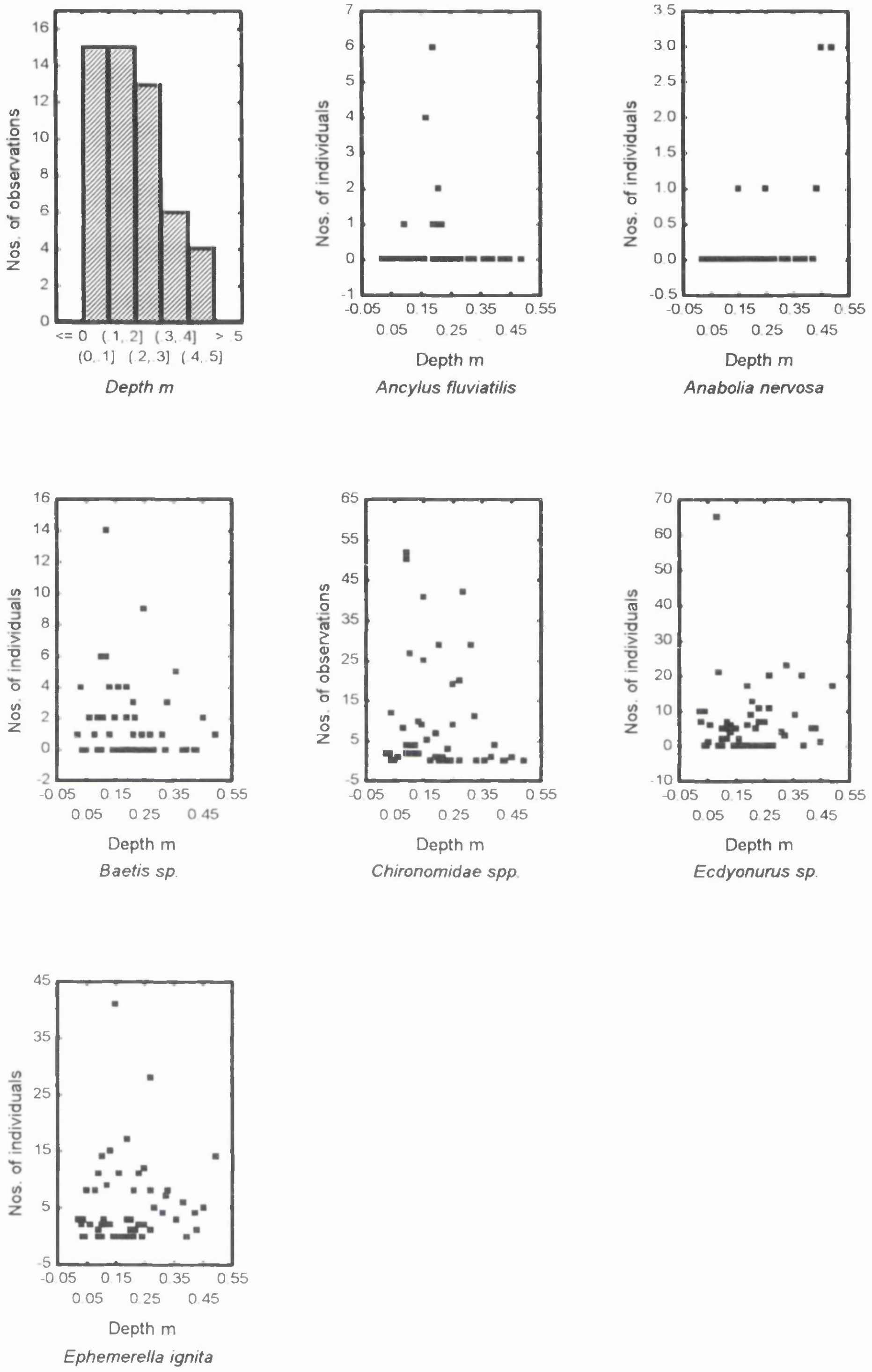
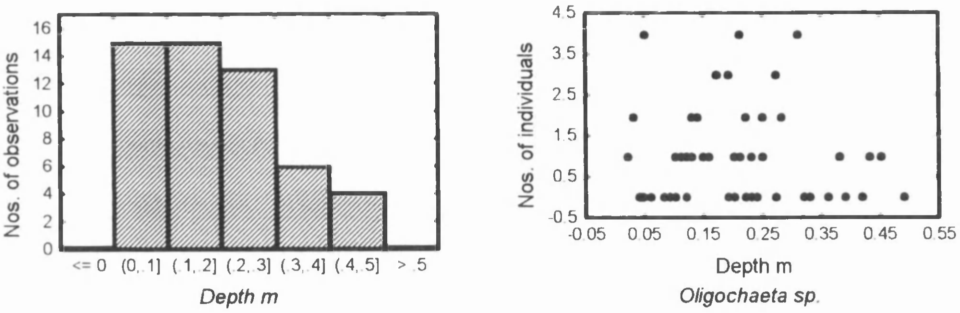
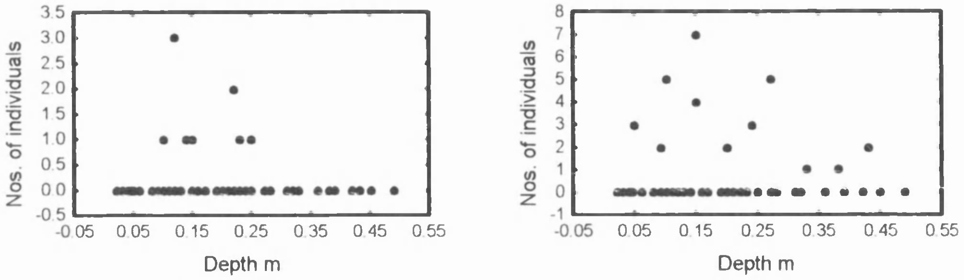


Figure 4-8a, Duneaton Water depth scatter plots with a histogram showing the frequency distribution of depth at sampling points. Abundance values are number of individuals per sample.

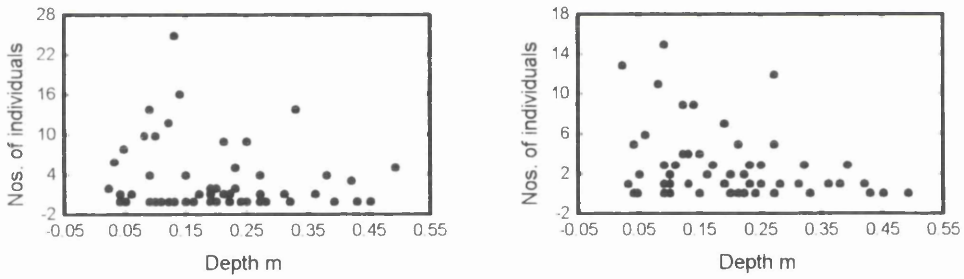


Oligochaeta sp.



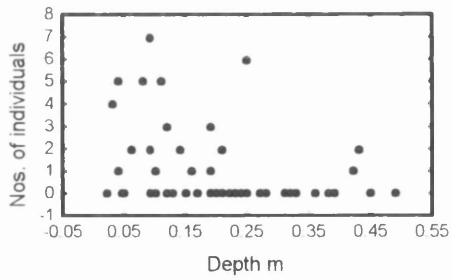
Hydropsyche sp.

Oulimnius tuberculatus



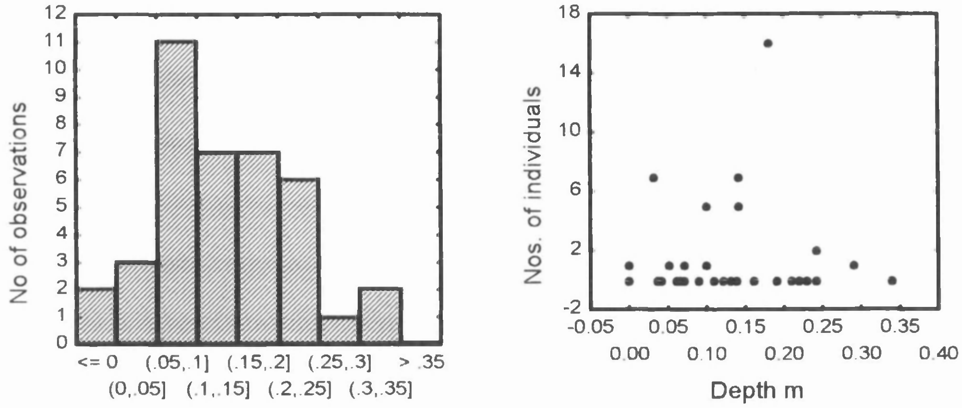
Leuctra spp.

Tipulidae spp.



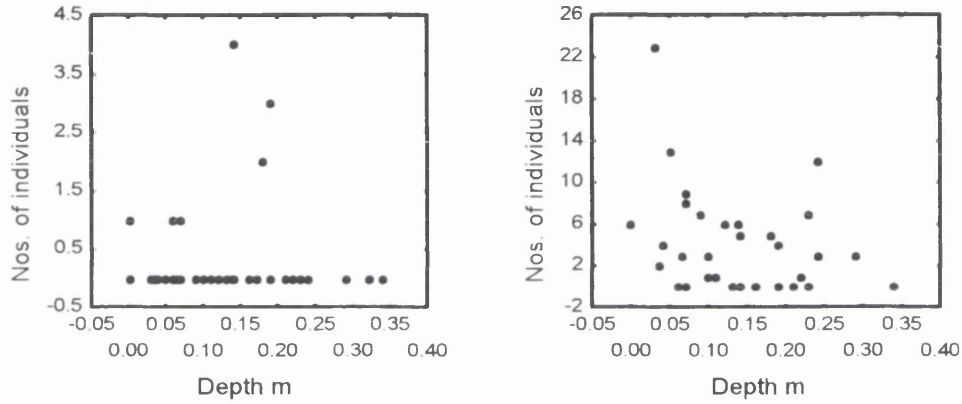
Limnius volckmari

Figure 4-8b, Duneaton Water depth scatter plots with a histogram showing the frequency distribution of depth at sampling points. Abundance values are number of individuals per sample.



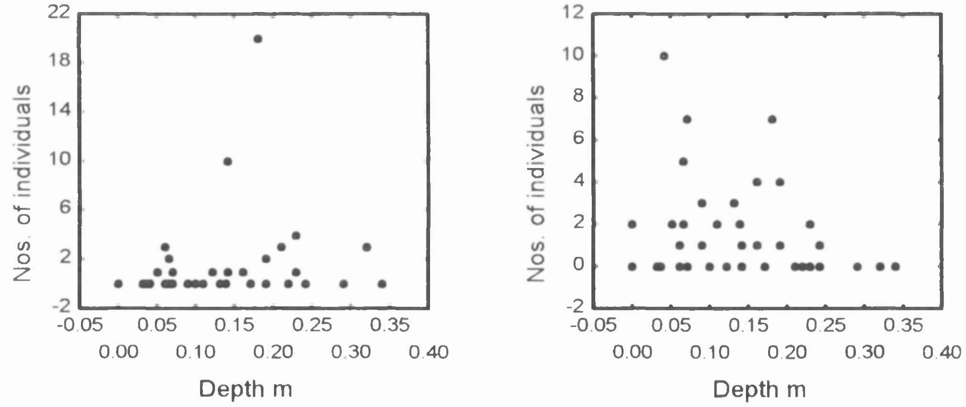
Depth m

Baetis rhodani



Agaptus fuscipes

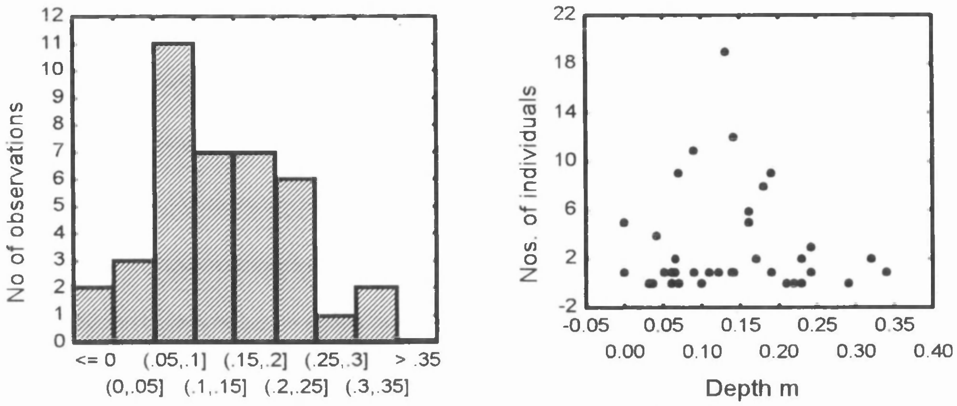
Ecdyonurus spp.



Ancylus fluviatilis

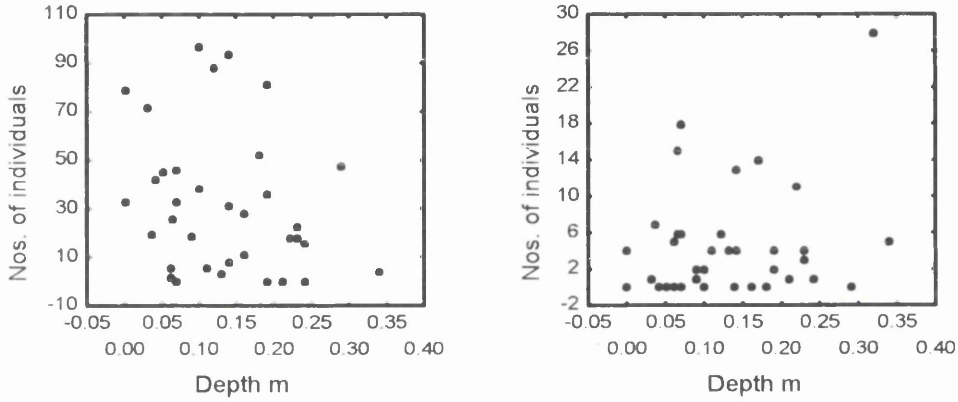
Elmis aenea

Figure 4-9a, Blane Water depth scatter plots with a histogram showing the frequency distribution of depth at sampling points. Abundance values are number of individuals per sample.



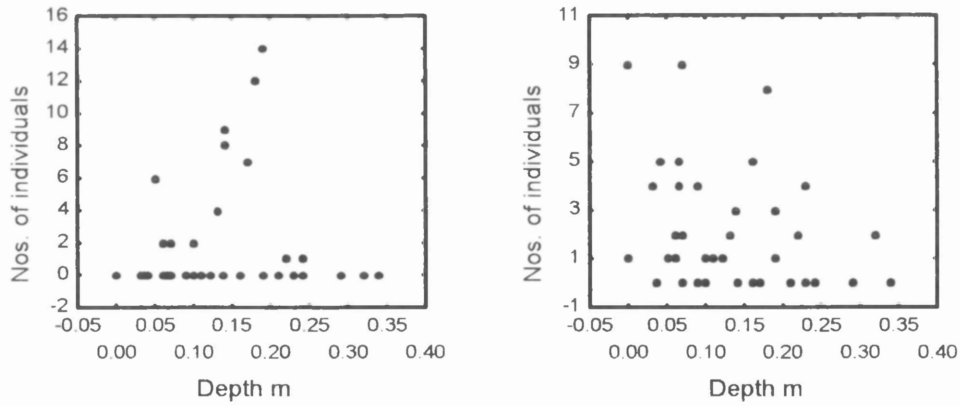
Depth m

Limnius volckmari



Ephemerella ignita

Leuctra spp.



Glossoma boltoni

Oulimnius spp.

Figure 4-9b, Blane Water depth scatter plots. Abundance values are number of individuals per sample.

4.3.5 Depth

River Etive

Of the three sites the R. Etive had the deepest sampling points extending down to 0.9 m, Fig 4-7a,b. Unfortunately because species occurred at very low abundances at the site, with some exceptions (*Hydroptila* spp. and Chironomidae), caution must be exercised in interpreting taxon responses. The majority of taxa (7 of 9) occurred in the highest numbers in samples which had the most frequently occurring depths, Fig 4-7 a,b. These taxa also tend to decrease in number mirroring the decrease in the availability of depths. Taxa exhibiting this type of response include, *Hydroptila, Baetis rhodani*, the Oligochaeta, Orthocladiinae and the Tipulidae. The maximum sample abundance of *Hydroptila* and Orthocladiinae were significantly correlated with available depths (Fig 4-2) while the totalled abundance of *B. rhodani,* Orthocladiinae and Tipulidae were also significantly correlated, Table 4-4. Both the Tanypodinae and the Chironomidae appeared to exhibit a preference for depths (0.4 m) just slightly greater than the most abundant ones. Both taxa were present in low numbers and caution should be exercised in interpreting these results.

Duneaton Water

The range of depths in the Duneaton Water was more limited than in the R. Etive extending to 0.5 m, only Fig 4-8 a,b. All taxa followed the distribution of available depths occurring at maximum densities at samples which had the most frequent depths, of these *Baetis* spp., *Limnius volckmari, Oulimnius troglodytes* and the Tipulidae was the only taxon whose maximum sample abundance was significantly correlated with the frequency of depth classes Fig 4-2. However the totalled abundance of Chironomidae, *E.ignita*, the Oligochaeta, *Oulimnius tuberculatus* and the Tipulidae were correlated with available depths Table 4-4. *Ancylus fluviatilis, Anabolia nervosa* and *Hydropsyche* sp. were not statistically assessed as they were deemed to have too few occurrences. *A. nervosa* was the only taxon not to show a preference for deeper water, but, again this species occurred in low numbers so the result should be interpreted with caution.

Blane Water

Depth range at this site was even more limited than at the other two sites getting no deeper than 0.35 m, Fig 4-9a,b. The totalled abundance of *Ecdyonurus, E. Ignita, L. volckmari, Leuctra* and *Oulimnius* were all significantly correlated with available depths, Table 4-4. The maximum abundance of few taxa follow the available depths directly in the manner of those at the Duneaton Water. The only taxa exhibiting this kind of response are *Ecdyonurus* spp., *Elmis aenea* and *Oulimnius* spp. Of these the maximum sample abundance of *Oulimnius* was the only one significantly correlated with depths, Fig 4-2.

The majority (7 of 10) of the other taxa did exhibit a similar response occurring in the greatest numbers in samples of depths between 0.15 - 0.20 m which are very common depths in this data set, but just higher than the most abundant depths of 0.05-0.1 m. Taxa exhibiting this kind of response include *E. ignita, G. boltoni, L. volckmari, A. fuscipes, A. fluviatilis* and *B. rhodani*. Of these, *E. ignita* showed a preference for the deeper sections. *Leuctra* is the only taxon to show a definite preference for the deeper sections reaching maximum numbers at 0.35 m.

Cross-site comparisons

Taxa occurring at all sites

E. ignita sample abundance showed no significant relation to the frequency of depth intervals at any site, but its totalled abundance did at the Duneaton Water. In both the Duneaton Water and the R. Blane the animal appeared to follow the available depths although at the R. Etive it showed a preference for deeper water. Once again numbers in the R. Etive are low and were therefore not subject to statistical analysis.

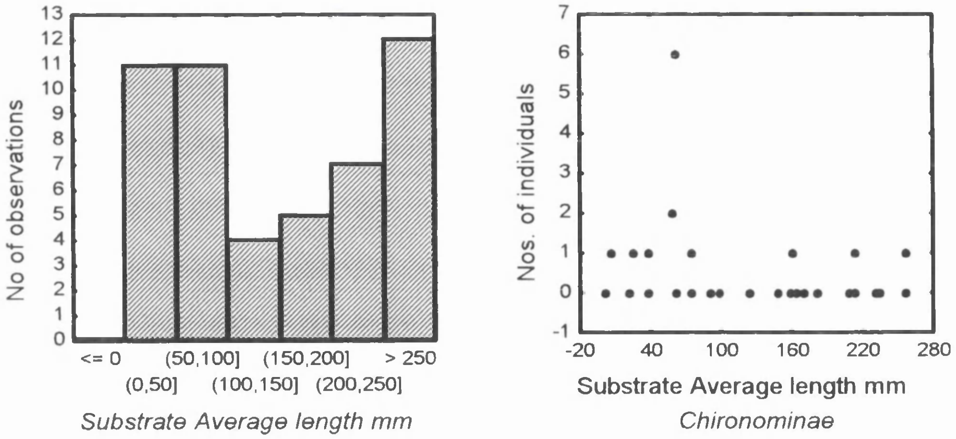
Limnius spp. at the Duneaton Water its maximum sample abundance was correlated with depth intervals, but its totalled abundance was not. This situation was reversed at the Blane Water.

Baetis spp. sample maximum was correlated with depth intervals at the R. Etive and the Blane Water and totalled abundance was correlated with depth intervals at the R. Etive too.

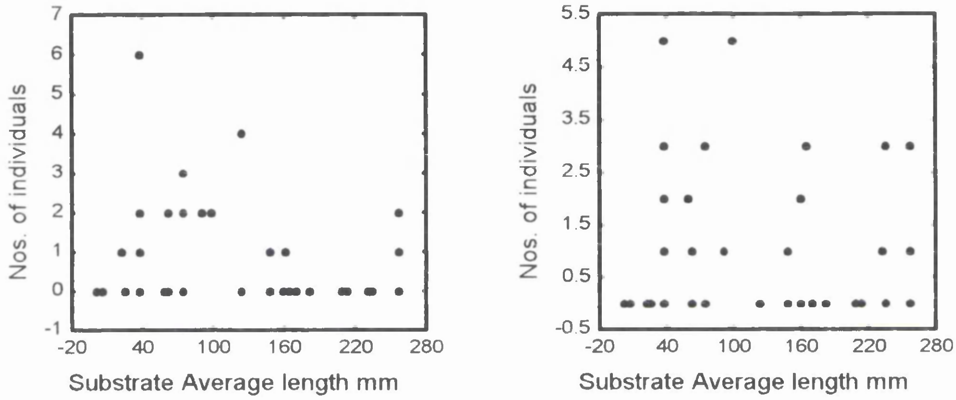
Duneaton Water and the R. Etive

Only at the Duneaton Water did Oligochaeta totalled abundance correlate with depth. A similar response pattern occurs at the R.Etive but was not significant.

At both the R. Etive and the Duneaton Water the totalled abundance of Tipulidae was significantly correlated with depth. Maximum sample abundance was also correlated with depth at the Duneaton Water.

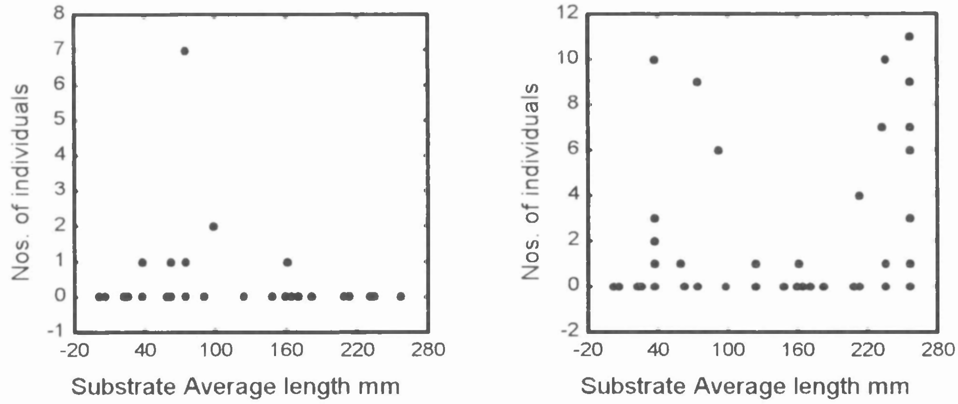


Chironominae



Baetis rhodani

Ephemerella ignita



Caenis rivulorum

Hydroptila

Figure 4-10a, River Etive substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.

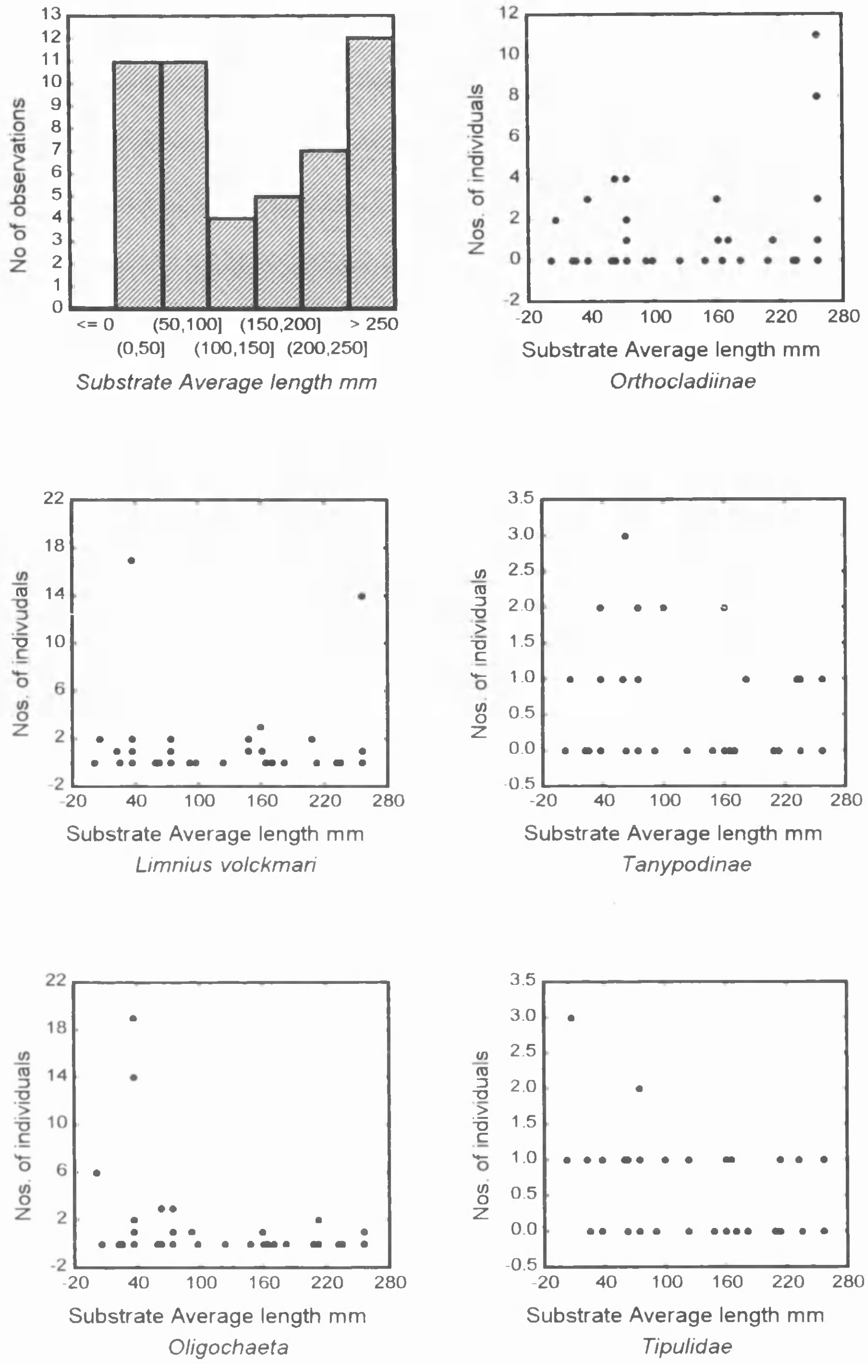


Figure 4-10b, River Etive substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.

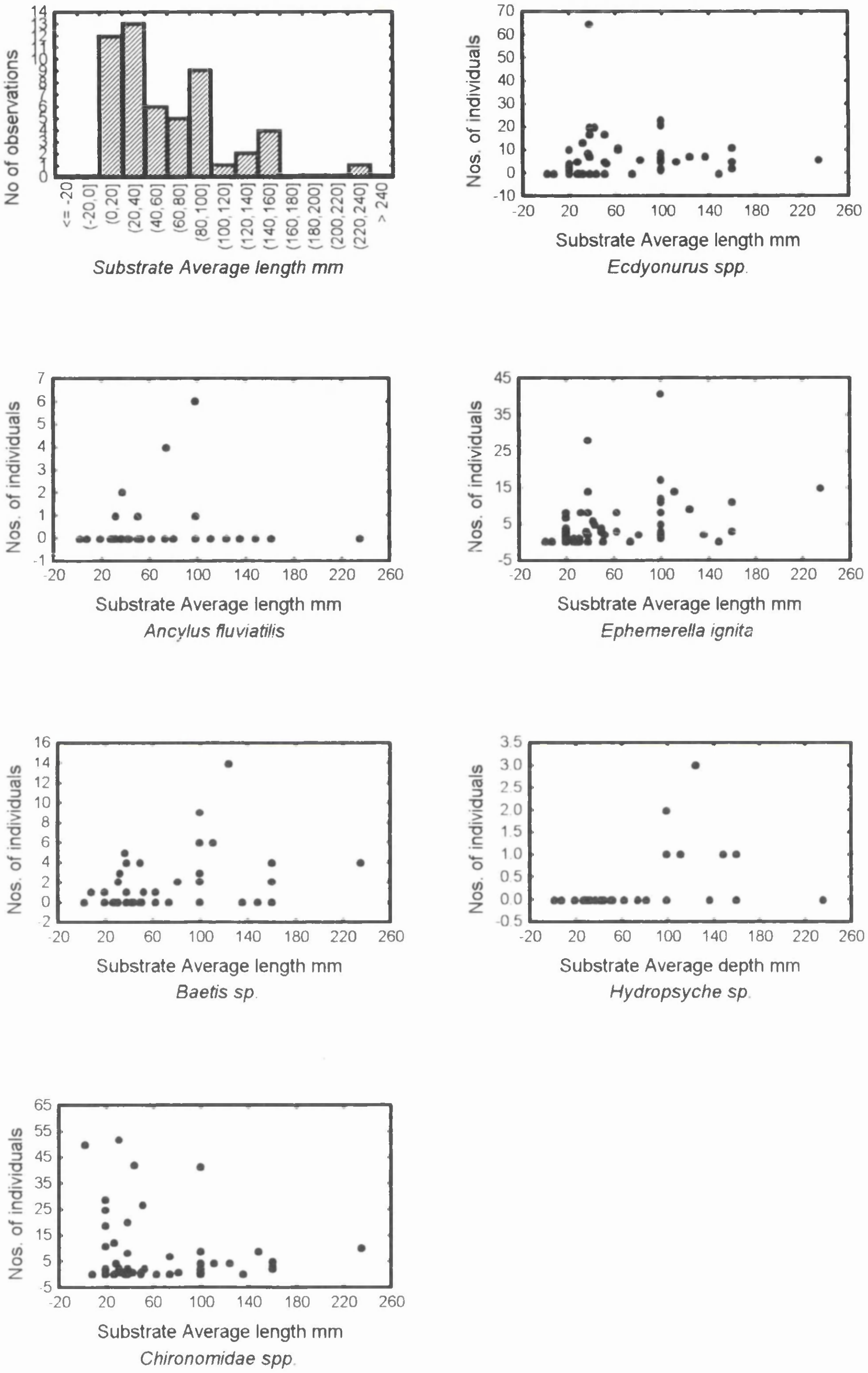
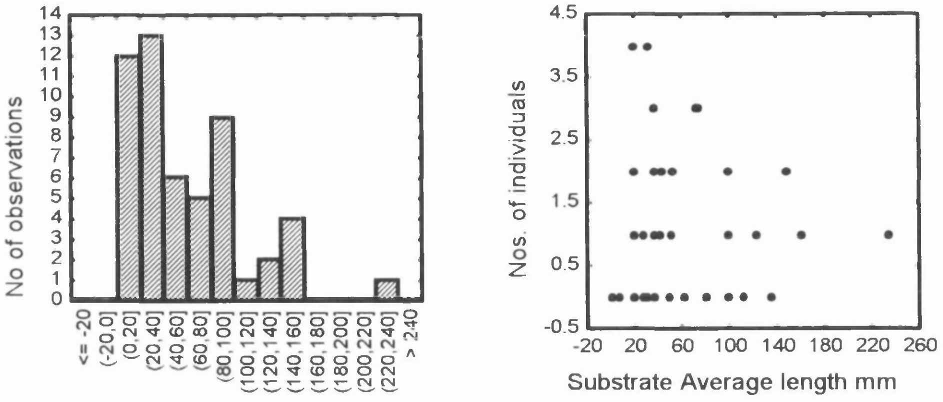
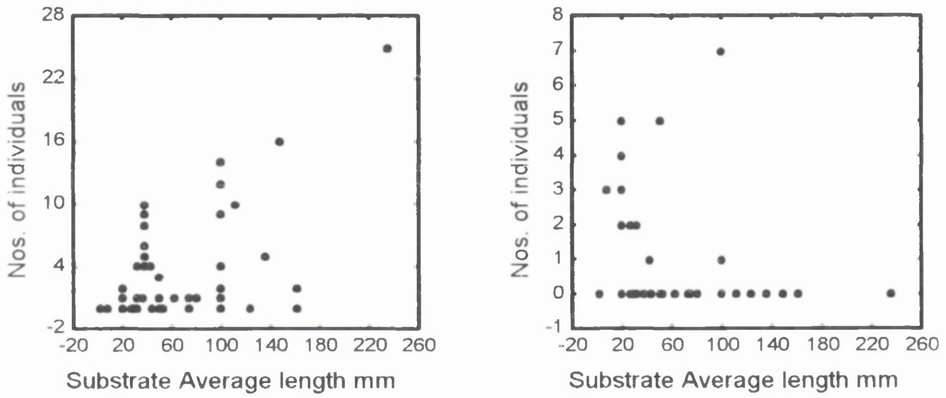


Figure 4-11a,Duneaton Water substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.



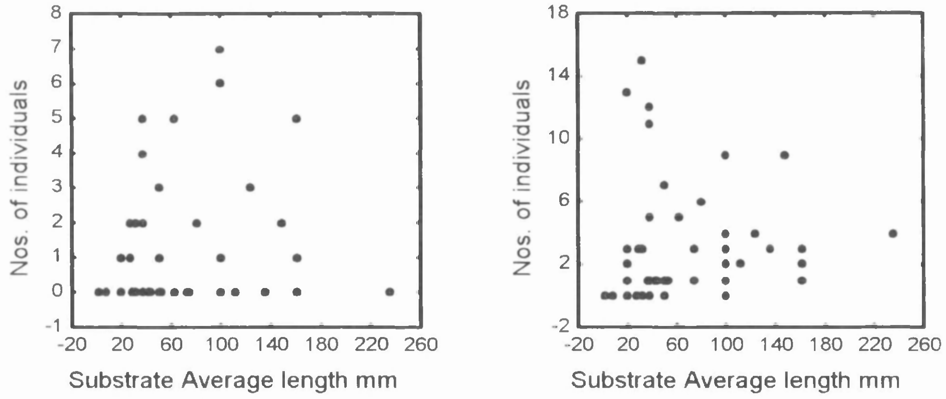
Substrate Average length mm

Oligochaeta spp.



Leuctra sp.

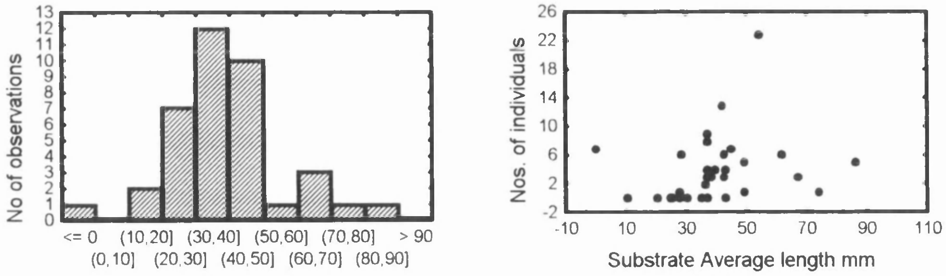
Oulimnius tuberculatus



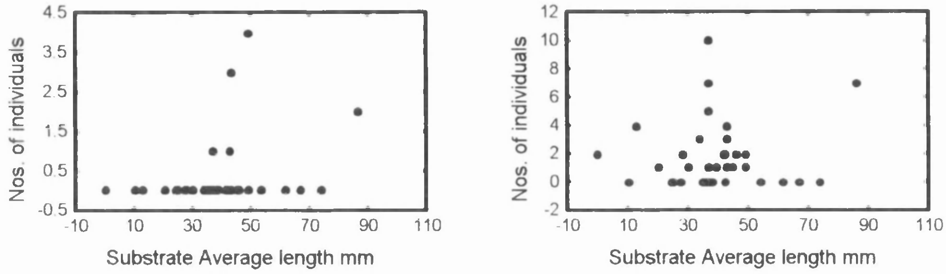
Limnius volckmari

Tipulidae spp.

Figure 4-11b,Duneaton Water substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.

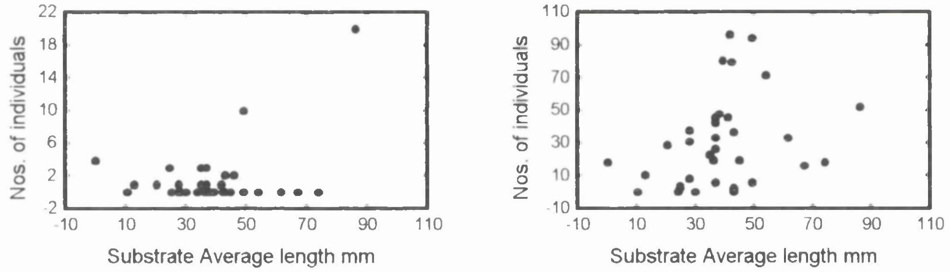


Ecdyonurus spp.



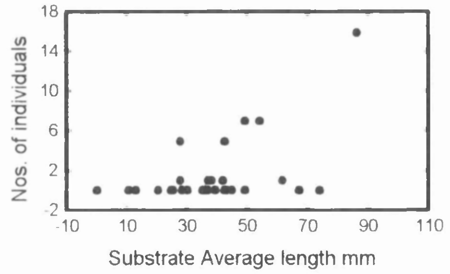
Agaptus fuscipes

Elmis aenea



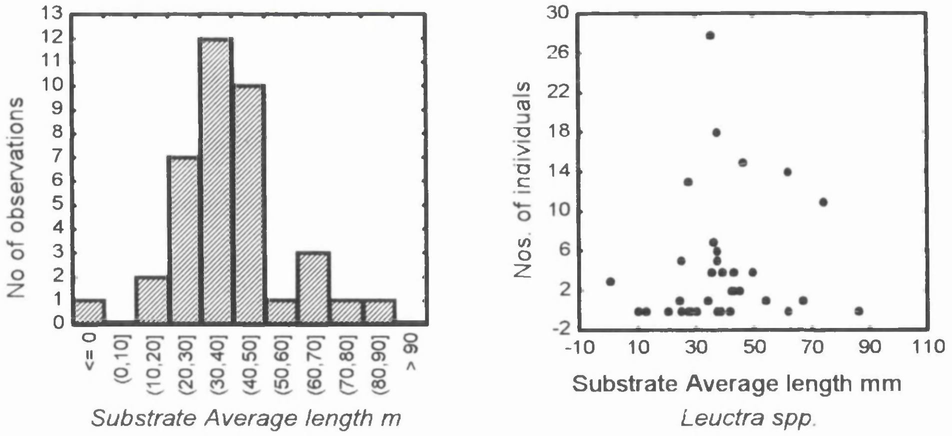
Ancylus fluviatilis

Ephemerella ignita

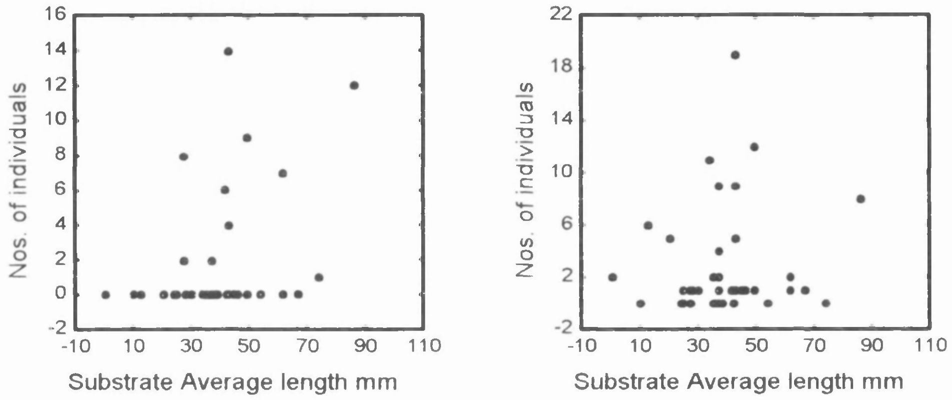


Baetis rhodani

Figure 4-12a,Blane Water substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.

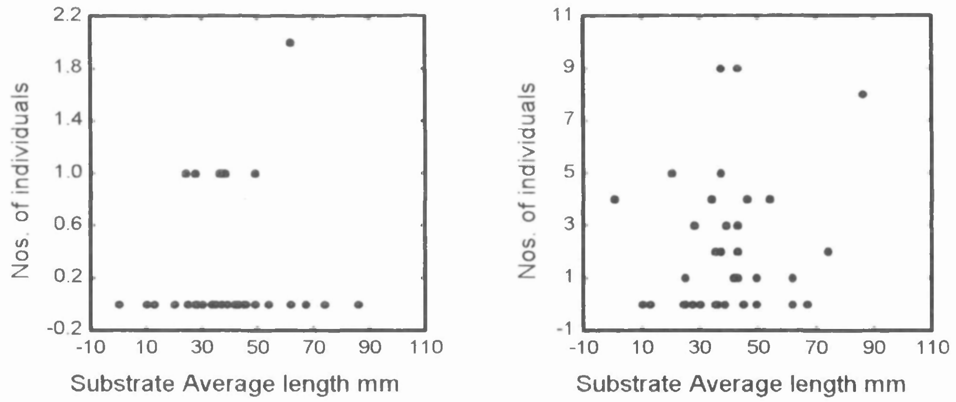


Leuctra spp.



Glossoma boltoni

Limnius volckmari



Hydropsyche siltalai

Oulimnius spp.

Figure 4-12b,Blane Water substrate scatter plots with a histogram showing the frequency distribution of substrate average length at sampling points. Abundance values are number of individuals per sample.

4.3.6 Substrate

River Etive

The distribution of substrate in the R. Etive was bimodal reflecting the high proportion of both fine substrates and, at the other end of the scale, boulders and bed rock, Fig 4-10a,b. Only the maximum sample abundance of *Hydroptila* spp. was significantly correlated with substrate intervals at this site, Fig 4-3. The highest abundances of other taxa are predominantly at the lower end of the substrate size scale. The Orthocladiinae were the only exception having two samples with relatively high abundances in samples dominated by larger substrate elements. The totalled abundance of none of the taxa present showed a significant correlation to substrate intervals.

Duneaton Water

Availability of substrate lengths decreased with increasing length of substrate elements, Fig 4-11 a,b. The maximum sample abundance of three taxa was correlated with the distribution of substrate intervals; Chironomidae, Oligochaeta and Tipulidae. For the last taxon the relationship was very strong, Fig 4-3. The other taxa show a range of responses; the maximum abundance of *Leuctra* spp. for example appeared to be inversely related to average substrate length, but this relationship was not significant. *Oulimnius tuberculatus* occurred predominantly in finer substrates while *Baetis* spp., *Ancylus fluviatilis, Limnius volckmari, Ephemerella ignita* and *Hydropsyche* larvae all appeared most abundant at around an average substrate length of 100 to 120 mm. The totalled abundance of none of the taxa present showed a significant correlation to substrate intervals.

Blane Water

The distribution of substrate was unimodal and therefore different from that at the other two sites, Fig 4-12 a,b. The range of average substrate lengths was much less here reaching only 90 mm. A high proportion of the taxa exhibited unimodal type responses but only the maximum sample abundance of *Leuctra spp.*, *Limnius volckmari* and *Oulimnius* spp. were significantly correlated with the availability of substrate intervals, Fig 4-3. These 3 taxa plus *B. rhodani* and *E. ignita* had their totalled abundance related to the distribution of substrate intervals, Fig 4-4.

4.4 Discussion

Despite the limited success of fitting Gaussian response curves to the data it is clear that many of the taxa exhibit unimodal or linear responses to the data. Where curve fitting was possible some of the taxa exhibited what appears to be bimodal distributions. This is likely to be a sampling artifact as the lower velocities and depths were sampled more frequently than the higher velocities / deeper depths, increasing the chances of animals being sampled there. Given that the higher velocities and deeper depths are less frequent and these taxa occur in relatively large numbers at these points suggests that these areas are actively sought out, e.g. it is likely that *Oulmnius tuberculatus* has a preference for faster waters.

When the taxa exhibit a maximum density in relation to a flow variable they frequently occur at lower densities at the same measure of that variable, i.e. in the Blane Water *Limnius volckmari* has a maximum density of 18 at a depth of 15 cm but it also occurs at a density of 1 at that depth. This factor would have reduced the correlation coefficients of the regressions.

As others have used alternative measures of abundance, including biomass (Makipaa 1999) or even using presence/absence in combination with logit regression (Saetersdal & Birks 1997) for other groups suggest a certain flexibility in approach. I would therefore advocate the use of maximal or summed abundance values, depending on the question being asked, as possible alternative values.

The responses of individual species indicate a close correlation with the distribution of the environmental variables measured. What is clear from the results is that often when an animal is dependent on the distribution of the environmental variable its maximum sample abundance is too. This suggests that the taxon is either adapted to the ambient conditions at the time of sampling or there is a statistical relationship between the chance of getting a sample with a high number of individuals in it and the number of samples at a particular point along the environmental gradient. Given the dynamic nature of the variables measured, particularly velocity and depth it would seem unlikely that the animals are that specifically adapted to the ambient conditions at the time of sampling. That most of the taxa have a broad tolerance for depth and mean water column velocity would seem most likely. Given that some of the same taxa exhibit this kind of response at different sites to different variables over different sections of the gradient supports the case for a statistical artefact. This is particularly obvious at the R. Etive where abundance was low compared to the other sites. The maximum sample abundance of some taxa showed strong correlations to the distribution of velocity intervals. When compared to the other river where the species occurred (the Blane) it was clear that the animals were within their natural tolerance range and could reach much higher abundance.

It would seem advisable in future work to have a non-random sampling strategy and take equal numbers of samples along the environmental gradient in question. Where a stratified sampling regime has been used it was more successful at identifying microdistributions of Hydrobiosidae larvae than the results shown here (Collier *et al.* 1995). The stratified sampling regime had been based on obtaining combinations of velocity and depths in the range of 0.1 - 1.5 ms^{-1} and 0.1 - 1.5 m respectively, using five increments. Unfortunately some combinations of velocity and depth were difficult to obtain leading to 'over sampling' of some combinations. This is a situation likely to occur in Scotland too. However, retaining the use of maximum sample values and relating them to intervals of the environmental gradient would help to control for any bias in the sampling.

This chapter is not meant to suggest that general survey work should not be carried or that it cannot be used to identify species-habitat relationships, rather that care should be taken in interpreting the results of such survey work in a quantitative manner, e.g. CCA analysis has the capacity to identify relationships between organisms and environmental variables even with this type of data. This is particularly the case for PHABSIM studies were the results can be used to control discharge from reservoirs. There is not only the chance that the incorrect ecological flows will be released but that by releasing too much water the reservoir managers will lose money; water is money.

One alternative option for survey work is to concentrate on a single or few species. This type of study can be very successful at identifying the spatial distribution of benthic invertebrates and related flow preferences (Cudney & Wallace 1980; Waringer 1987).

4.5 Conclusions

- Data collected using Instream Flow Incremental Methodology on benthic invertebrates should not be used to model available hydraulic habitat.
- Structured sampling regimes need to be used if species flow preference curves are to be recorded correctly.

Chapter 5: Flume experiments: entrainment velocities of benthic invertebrates

5.1 Introduction

The expression of an animal's tolerance of an environmental variable as being bounded by a minimum, optimum and maximum is not only intrinsically satisfying but also useful in the field of water quality management and restoration projects (Peeters & Gardeniers 1998). Water movement is a fundamental environmental variable in lotic systems and can be viewed as the main engineer of the system habitats (Petts *et al.* 1995). Of the various aspects of water movement velocity is the most temporally variable. The aim of the work reported in this chapter was to accurately measure the capacity of different invertebrates to resist entrainment. The point at which this occurs can be viewed as the animal's upper tolerance limit for velocity.

Of the three measures, the upper tolerance was chosen as the most useful. Managers controlling regulated rivers frequently need to release water from dams for maintenance and water level control behind the dam wall. These releases presumably exceed the upper flow tolerances of macrobenthos because they are known to cause considerable disturbance of community structure in the receiving channel (Dejalon & Sanchez 1994). The lower tolerances of the animals are likely to be provided by the release of Q90 or Q95 flows, a SEPA requirement requested during the planning process for the discharge below dams in Scotland (Town and Countryside Act 1997). Determining the optimum velocity for stream benthos, although attractive, is difficult to measure in the field and artificial channels, particularly for the more mobile taxa.

The capacity of benthic invertebrates to withstand high velocities has repeatedly intrigued researchers. Some very early work had excellent observations on the importance of shape and behaviour of aquatic insects in withstanding entrainment

(Dodds & Hisaw 1924; Dodds & Hisaw 1925). When the upper velocity tolerances of individuals were actually measured, variations in results between workers were considerable (Dittmar 1955; Dorier & Vaillant 1955) leading Hynes (1972) to observe that laboratory experiments were not particularly informative, probably due to the unnatural conditions to which the animals were exposed. There are probably many reasons for the inconsistencies observed, the most obvious being that the velocities measured were not recorded in front of the animals, but further up in the water column (Dittmar 1955; Dorier & Vaillant 1955). Other complicating factors include the fact that the animals were on different substrates. Neither of Dittmar's studies reported the depth at which velocity measurements were made so it was impossible to calculate Reynolds number (which would have allowed more direct comparisons). Although some studies did calculate the force of water incident to the animals, the measurements were not taken from in front of the animals. To compound the difficulty with interpreting these results, some of the experiments were carried out in circular flumes where vortex forces apply (Bournaud 1963). The accuracy of the results is therefore questionable.

An increased awareness of invertebrate drift stimulated large numbers of flume and field experiments which began to accumulate the lengthy list of factors which can influence drifting. Velocity and substrate are included among these factors (Ciborowski 1983; Holomuzki 1996). The majority of flume experiments avoided studying the responses of individuals looking at groups on animals instead, but did report on the importance of density; drift does increase with density. (Borchardt & Statzner 1990; Ciborowski 1983; Ciborowski 1987)

Some experiments looked at drift under extreme flow conditions in flumes, but again the interest was not in individual capabilities (Lancaster 1992). Rather, the interest was in the importance of disturbance events. Whilst it was clear that both natural and human simulated spates had the capacity to cause animals to drift (Matthaei *et al.* 1997; Matthaei *et al.* 1996), it was not until later that it could be shown that animals could avoid being washed out of the system by accumulating in refugia (Lancaster & Hildrew 1993a). Both active movement and passive drifting were observed (Lancaster 1999) which contributed to no net loss in animals from spate channels and control channels if refugia were present. This capacity helps to explain the exceptionally fast rates of recolonisation that are observed post spates (Death 1996). The circumstantial evidence was mounting that animals were not only being entrained passively, but would actively enter the drift. Supporting evidence already existed since it had been shown that baetids drifted in response to the distribution of food resources within experimental areas in artificial channels (Kohler 1985).

An animal can choose where it is going but, by drifting, the animal would appear to forfeit control of its choice. This view is repeatedly seen in the work that does concentrate on individual animal responses to extreme flow conditions.

Laser Doppler Anemometry (Statzner & Holm 1982) proved that a laminar sub-layer would be too thin to afford protection to invertebrates from turbulent flow, which was contrary to the long held understanding that they could (Ambuhl 1959). It was necessary, in light of this discovery, to explain how animals resisted entrainment. Reviews prior to Statzner's discovery concentrated on the anchoring equipment and streamlining of animals (Hynes 1972). Now the concept of drag was introduced (Statzner 1988). As Vogel (1994) states 'it is easy to define drag as the removal of momentum from a moving body by an immersed body' but 'where in it does shape enter?'. Some animals are streamlined, others flattened, in attempts to reduce drag but it has been pointed out that such adaptations can have counter-intuitive implications i.e. flattening can cause positive rather than negative lift which has the potential to lift the animal off the substrate (Vogel 1994). As drag and lift are not the only factors affecting the animals it became clear that any animal shape is a compromise (Statzner & Holm 1989) and the need to acquire food also can conflict with the demand to reduce drag (Hart 1991). Even the different instars have different ideal drag-reducing shapes because they live at different Reynolds numbers (Statzner 1988). The need to compromise means that either structural anchors (claws or suckers) and muscle power must be used to avoid entrainment. *Ecdyonurus* can achieve negative lift as its legs act to produce a downward force, but it is likely that it must remain static to achieve this because any movement would mean altering the angle of the legs presented to the on coming water (Weissenberger *et al.* 1991). Any movement from that location would require energy to be expended, unless the animal was to actively drift out of this position. The attachment mechanism of water pennies does allow movement across rocks exposed to high velocities with potentially limited effort, but this is likely to be a rather exceptional case as this taxon spends most of its time on the underside of stones (McShaffrey & McCafferty 1987; Smith & Dartnall 1980).

A simple measure of the energy required to resist entrainment was calculated by subtracting the animals' passive resistance to drift (when dead) from its active (live) resistance (Waringer 1989b; Waringer 1993). This approach was not new: Walton (1978) had also compared dead and live animals. This was achieved by accurately measuring the animals' frontal area exposed to oncoming flow and calculating the velocity to which it was exposed across this area at entrainment. The relative importance of the animals' shape and muscle power were not assessed. However the results of the analysis did predict the distribution of some of the animals in the field (Bacher & Waringer 1996; Waringer 1989a). Waringer's field data suggested

Allogamus auricollis Pictet should never occur outwith areas where it could resist flow passively, although this was not the case for other Trichoptera. This suggested that the situation was complex and that apparently similar species could behave rather differently in real systems.

I decided to attempt this experimental approach. It not only gathers data on the upper velocity tolerance of the individual animal, but gives some idea of the energy it must expend to avoid entrainment. This is done by calculating the force exerted on the frontal area of the animal by the moving water. I wished to extend the observations to groups other than the Trichoptera. In reality, my success was limited for a number of reasons. The principal difficulty was in obtaining accurate measures of velocity incident to the frontal area of the experimental animals. However some potentially useful data were obtained, and are presented here.

The experiments presented here tried to repeat Waringer's work, but use Ephemeroptera, Crustacea and Diptera, the aim being the same to determine the amount of effort the animals put into maintaining position and to find the highest velocity to which they are tolerant. The morphometric measurements were made on the animals, but are reported here for only one of the animals; *Ecdyonurus* because problems with the methodology prevented the study being extended to other species, (see section 5.2.1).

Due to difficulties measuring accurately the upper velocity tolerance limit, and the animals' apparent ability to drift over a range of velocities, a different approach using logistic regression, was adopted to show the range of drifting velocities for the animals. This formed the second aim of the chapter. Logisitic regression shows, in graphical form, the probability of the animals drifting over a range of velocities, and was the method adopted here. The hypothesis being that with increased water velocity the chances of the animals becoming entrained increases.

So to conclude the real aim of this chapter is to present some results salvaged from attempts to replicate Waringer's experiments. Morphometric relationships between head width and head frontal area are presented for *Ecdyonurus*. Observations on the behaviour of benthic invertebrates exposed to high water velocity made during the experiments are presented. Some data is presented on the phototrophic responses of the study animals (light was to be used as a non-invasive stimulus during the experiments). Finally logistic response curves of *Gammarus pulex* and Tipulidae to water velocity and the influence of body weight on this response, for the Tipulidae.

5.2 Materials

5.2.1 Flumes

5.2.1.1 Waringer's Flume

A bench top flume designed and described by Waringer (1989b) was built but a number of difficulties were encountered in accurately calculating velocity. Firstly, it proved impossible to use conventional flow measuring techniques because water depth was limited to < 0.05 m in most areas. The flow measurement technique used by Waringer corrected surface velocity, measured with a piece of floating polystyrene, to velocity deeper in the water column i.e. in front of the animals.

To use this method at higher velocities a video camera was mounted above the flume which recorded the movement of the polystyrene ball over a fixed distance marked on the flume floor. On play back, the number of frames could be counted and since the time length of each frame was already known, velocity could be calculated.

To correct surface velocity to that occurring directly in front of experimental animals Waringer used diagrams relating water depth to velocity in Dingman (1984), not the equations quoted in the paper (Waringer pers comm). These equations can only be applied if the Reynolds number (Re) for a point in the flume can be calculated and this is not possible from the data. Waringer calculated Re using the diagrams given by Dingman (1984). However one cannot apply these diagrams unless the Re is known: the argument seems uncomfortably circular. Secondly the diagrams can only be applied to areas of steady flow. Steady flow describes flow where velocity at a point is constant or varies in a predictable manner, all fluctuation in flow is at a molecular level (Walker 1995). Flow in the flume constructed at Glasgow proved to be unsteady, due to the creation of a hydraulic jump near the start of the channel. This led me to reappraise the flow-measuring techniques used above. Flow was also unsteady because the flume widens toward its end, so depth and velocity vary constantly. Alternative methods of measuring flow including the use of dyes did not prove successful. An alternative flume was required which had the capacity to produce velocities of >1.5 ms^{-1}, and permit the use of standard electromagnetic velocity meters Such a flume is described below.

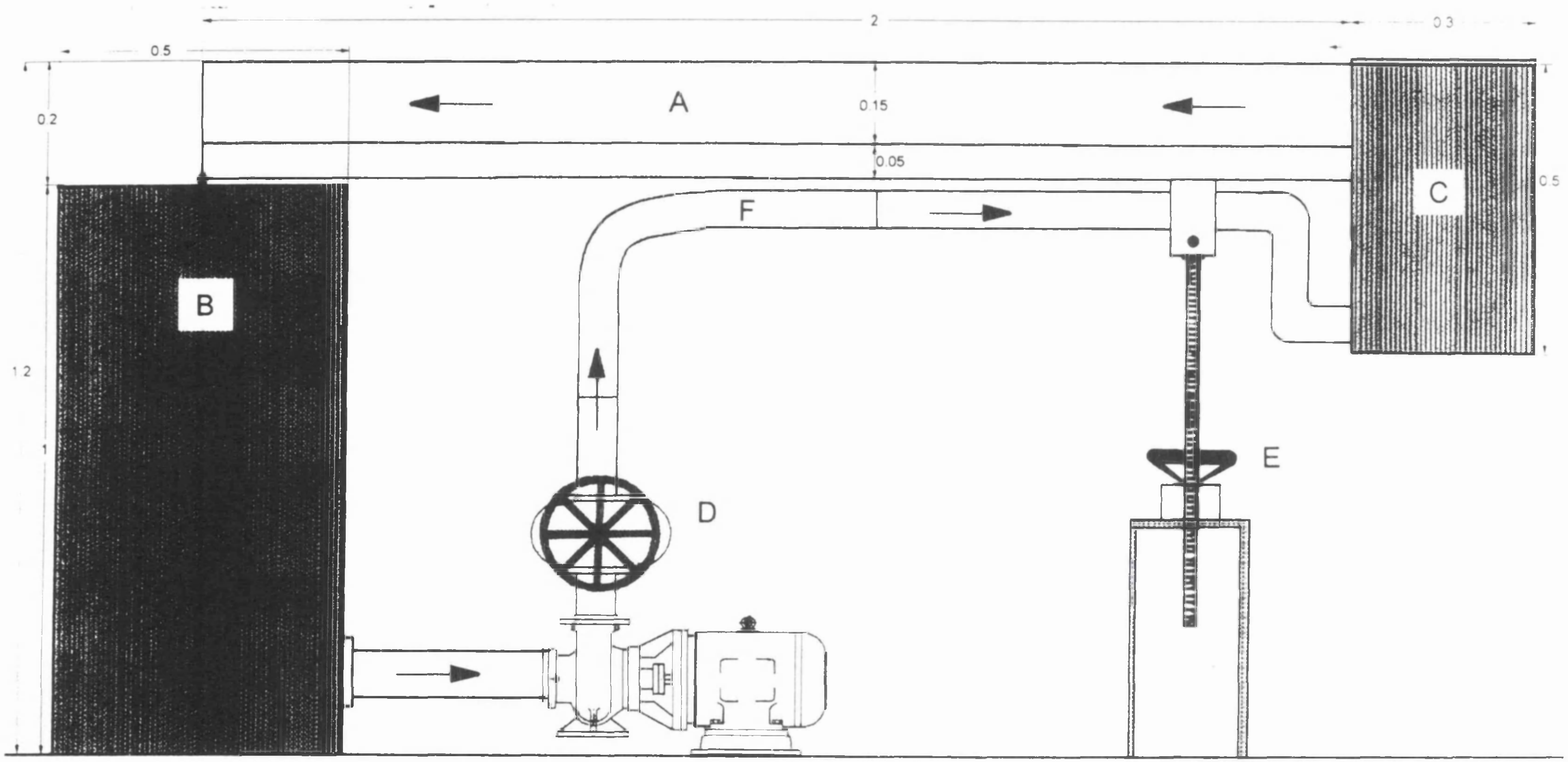


Figure 5-1, Rowardennan flume, side elevation. Units are m. A, experimental channel, width 0.1; B, Main reservoir width 0.5; C, Small reservoir containing flow homogenising marbles, width 0.1; D, Gate valve; E, Adjustable height support and F, flexible tubing.

5.2.1.2 Rowardennan Flume

Most of the experiments were carried out in a narrow flume 0.1 m wide, (Figure 5-1). The water circulatory system is closed. Water was aerated by falling from the experimental channel into the main reservoir. This process was sufficient to keep the water saturated with oxygen during all operations; dissolved oxygen was measured using a field probe (Hanna Dissolved Oxygen meter 1997 model). The flume was housed in an unheated shed at the University field Station loch lomondside, under low light intensities, and at ambient temperature. Water was supplied from Loch Lomond (pumped from c. 10 m below the surface and 200 m from the shore). The water was untreated, but was filtered through a phytoplankton net before use. The operation of the pump could increase temperature by 1-2°C per hour and, when this occurred, the water was replaced.

Discharge to the experimental channel was produced by a pump working at 12 ls^{-1} and controlled by a gate valve. This allowed a very fast increase in discharge if required. The slope of the channel could be altered by adjusting its height. Flow was homogenised through a bed of marbles placed in the small reservoir. Depth in the channel was controlled by means of 0.02 m high perspex blocks which could be slotted into the end. A zooplankton net was placed over the mouth of the main reservoir to collect any animals swept out of the channel during experiments.

5.2.2 Flow Structure in the Flume

Flow in the channel varied gradually along its length, which was too short for steady uniform flow to develop (i.e. flow was not full developed: the boundary layer did not extend to the surface, but only partially through the water column, e.g. to a depth of 3 cm above the floor near the end of the flume). Estimation of velocity at different heights above the bed using velocity profiles required the identification of the height of the boundary layer. In the boundary layer, the log-normal relationship between velocity and depth applies and can be used to estimate velocity at different depths, i.e. in front of an animal. Above the boundary layer velocity, does not vary with depth so no estimation process is necessary.

To calculate the force of water acting on the surface of the animals we can apply equation 6.32 from (Dingman 1984).

$$u = 2.5U^* \ln(\frac{9.00U^* y}{v})$$

Where u is the velocity at depth y (See Appendix I for definitions of terms)

This equation applies to hydraulically smooth flow, as is the situation when contact is made with the substrate. It was developed for wide channels rather than the narrow flow and channel used in the present experiments. As a result, their assumptions for calculating U^* are not valid. Instead, U^* in gradually varying flow is

n = Mannings n for the channel

S_f = Slope of the energy line

$$U^* = \sqrt{gRS_f}$$

$$R = A/P$$

$$S_f = \frac{n^2 \overline{u}^2}{R^{4/3}}$$

$$U^* = \sqrt{g \frac{n^2 Q^2}{A^2 R^{1/3}}}$$

This replaces S_f for S_o, where S_o = Channel slope tangent.

Manning's n was estimated as 0.01 for flume with Perspex sides.

Equation 6-33 in Dingman (1984) can be applied for rough flow but k_s would have to be calculated.

Both equations 6-32, and 6-33 in Dingman (1984) are for fully-developed flow but can be applied to the case in question here since we are only interested in the region of developed flow at the bottom of the water column (D.A. Ervine, Glasgow University pers comm).

5.2.3 Animals

All of the species used are common in Scotland and are sufficiently abundant in rivers to provide numbers for experimental analysis. The mayfly taxa *Baetis rhodani* and, *Ecdyonurus,* the dipteran Tipulidae, and two crustacean species *Gammarus pulex,* and *Asellus aquaticus* were all used. It was not possible to identify the *Ecdyonurus* larvae to species but they were either *E. torrentis* or *E. dispar*, both of which were present at the site. During some of the later work adults emerged: all were *E. torrentis*. The Tipulidae were all of one species as yet not identified as no keys are available to identify this larvae to species. Specimens have been retained and it is hoped to rear some larvae of the same species to adulthood this year. Keys do exist for identifying adults. All animals were collected from the Blane Water (site description, Chapter 2 Section 2). Animals were collected by a number of means, usually stones were turned over by hand and the animals allowed to float downstream into a pond net. Where animals remained on rocks they were gently removed either with the finger or an artist's paint brush to prevent damage to their cerci and other appendages. Animals were transported to the field station in containers of river water which were aerated using a portable air pump. On arrival, they were immediately transferred to communal tanks (0.3 x 0.2 x 0.15 m), one tank per taxon in the shed housing the experimental flume, which were also constantly aerated. Water was changed in the tanks every 2 -3 days. Animals were not fed during their captivity but none were kept longer than a week. Mortalities were infrequent.

5.3 Methods

5.3.1 Weighing and Morphometric Measurements

Animals were removed from their holding tanks, carefully dried on absorbent paper then weighed. Subsequently they were observed under a binocular dissecting microscope and the head width measured using an eye piece micrometer. Animals were then transferred to individually numbered plastic cups and remained in the flume shed until they were used in the experiments. Tipulidae lasted in this type of confinement without any reduction in observable health for up to a week, *Gammarus pulex* and *Baetis rhodani* remained in good condition for approximately 4-5 days.

For *Ecdyonurus,* head width was related to the frontal area that would be exposed to the current. After measurements of head width had been made, the animals were then killed and mounted on to pieces of card which were covered in nail varnish. Animals were posed on the card in a position assumed by *Ecdynonurus* when resisting entrainment, as observed by Weissenberger et al. (1991). Animals were placed facing a binocular microscope lens to which a video camera was attached which was, in turn, linked to a computer, Figure (5-2).

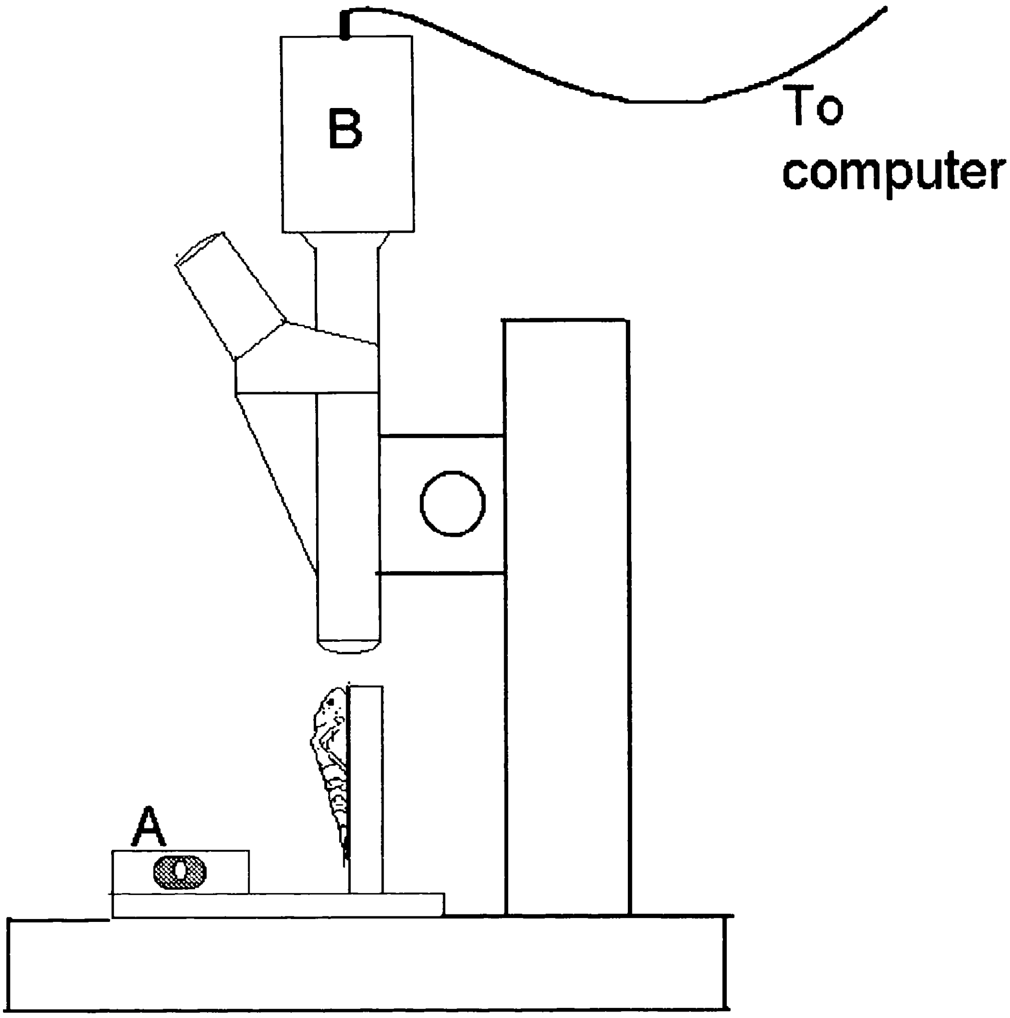


Figure 5-2, Measurement of *Ecdyonurus* frontal area. Binocular dissecting microscope. A, Cast iron right angle mount for specimens with built in spirit level; B Video camera linked to computer.

An image of the animal was recorded using a frame grabbing video card and then analysed using Sigma Plot software. The image of the animal was outlined by hand and then filled: the irregular filled area could then be measured using the computer program. Pixels. Counts were transformed into SI units using a calibration based on measurements taken with a slide micrometer.

5.3.2 Experimental design and Statistical Analysis

In all the experiments carried out, randomisation of treatment order and allocation of individuals to treatment was used to avoid any experimental bias. Hurlbert (1984) has suggested that randomisation procedures can inadvertently create patterns in the designation of experimental subjects to particular exposures thereby creating a bias that they were trying to avoid. After each randomisation procedure I checked to make sure no aggregations occurred. The main factor of concern was particular exposures aggregating at particular times of the day. All experiments were carried out in daylight hours and stopped before the onset of dusk.

Phototaxis:

All experimental taxa were first screened to determine their response to light. During some of the experiments which follow, a quantifiable stimulus was given to the animals to move upstream. Light was the only stimulus which would not interfere with water velocity around the animal and could be applied to specific areas of the flume. To determine the animals' responses under non-flowing conditions, the experimental channel was dammed at both ends and flooded to capacity. This exposure acted as a control for later experiments. A board was placed over the top of the flume, 0.3 m from its end and extended 0.5 m along the flume. Underneath this area the walls were blocked with card. A bench lamp with a 60 W bulb was then placed on top of the plank and shone toward the downstream end of the tank. This created a sharp border between the light and dark zones of the flume. As mentioned earlier, the flume hut had low background light levels. From groups of about twenty animals (depending on availability) individuals were placed singularly in the flume, on the border line and exposed for 3 minutes to moving water, or, in the case of the control, still water. Exposures were randomised as described above. Animals were placed parallel to the border line facing neither into the light nor the shade. Head width and weight of all animals was recorded. A non-parametric Mann Whitney U test was performed on the data for the *B. rhodani* groups responding preferentially to either light or shade. Statistical comparison between light and shade preferences under flowing water conditions were not performed. When exposed to running water the vast majority of the animals sought in the illuminated zone. Only a limited number of animals remained in the dark zone. It was clear that light was of secondary importance to remaining in the channel.

Rheotaxis and swimming

The initial aim of this work was not solely to observe the animals' behavioural responses to high water flow rates, rather it was to measure the upper velocity tolerance of the various taxa. Animals were placed in the flume individually on the border between the light and dark areas with the channel flooded and the water still. They were allowed to settle for five minutes and then some of the barrier at the end of the experimental channel was carefully removed in sections to prevent any surging motion in the water upstream which would inadvertently entrain the animal. The pump was then started and the gate valve, which had been kept completely shut, was slowly opened which allowed water to begin flowing gently. Velocity was increased slowly over 3 to 4 minutes by opening the gate valve further. When required, the experimental channel was also angled upward to increase velocity. This was necessary only in exceptional cases to achieve velocities over 1.2 ms^{-1} for ecdyonurids. When the animal became entrained it was recovered from the end of the flume and, at the point where entrainment occurred a velocity profile was measured at 10 positions through the water column, by taking 15s averages at each point. It soon became clear that the animals had an impressive capacity to find areas of the flume where velocity was low (near the walls) as refuges and that these locations were also inaccessible to the velocity meter. They also showed a willingness to drift over a range of velocities and appeared unwilling to expend energy withstanding entrainment. For this reason it was felt that measuring an upper velocity tolerance limit in this manner was not informative and only the animals' behavioural responses are reported.

Logistic response curves

The previous experiment determined the range of velocities at which the different taxa normally drifted and this allowed a new experiment to be designed which concentrated on determining the probability of animals drifting at different velocities. The velocity range of animals had been determined in the previous experiment. From the range a number of velocity 'exposures' were chosen (see Table 5-1). Animals were collected, weighed and measured as described above. They were then assigned to each exposure in a random manner, 5 animals to each exposure. Each animal was treated to its velocity exposure individually for a period of 3 minutes and then its behaviour was scored using the list of behavioural categories presented in Table 5-2. The order in which each exposure was made was completely randomised.

Frontal area to head width

To predict the frontal area of *Ecdyonurus* exposed to flow from its head width a simple linear model was used. Animals were chosen to cover the maximum range of head widths available.

Table 5-1 The velocity to which the three taxa were exposed.

Taxa	Number of exposures	Exposures ms^{-1}
Tipulidae	7	0, 0.04, 0.06, 0.08, 0.1, 0.12
Gammarus pulex	5	0, 0.10, 0.15, 0.20, 0.30
Baetis rhodani	4	0, 0.3, 0.5, 1.10

Table 5-2, Definitions of behaviour scored during exposures to velocity. Given in Table 5-1.

Behaviour	Definition
Entrained	Any movement downstream
Resisting flow	Struggling to remain in situ or moving to flume edge
Active	Moving upstream or lateral movement without any downstream movement
Inactive	Remaining still

Effect of weight on entrainment of Tipulidae

Animals were collected in the field as previously described. Animals were ranked in order of their weight. Of these, 30 animals were chosen covering the range of weights available. This equated to 1 individual representing every 0.01 g increment in weight. Each individual was exposed in a similar manner to a series of velocities: 0.04, 0.06, 0.07, 0.08, 0.10, and 0.12 ms^{-1}. The order in which the animals were selected for the experiments was randomised and the order an individual was exposed to the velocity intervals was also randomised. Animals would frequently become entrained at velocities below their upper velocity tolerance. The lowest and highest velocity at which an animal was entrained were recorded to take account of this behaviour.

5.4 Results

5.4.1 Head width to frontal area ratios

There was a positive significant relationship between head width squared and frontal area of *Ecdyonurus* ($p < 0.0001$, $F(1, 73) = 144.5$, $R^2_{adj} = 0.65$). Although the relationship was significant, there was fairly substantial degree of individual variation:

Frontal area = $-0.40 + 0.409(\text{Head width})^2$.

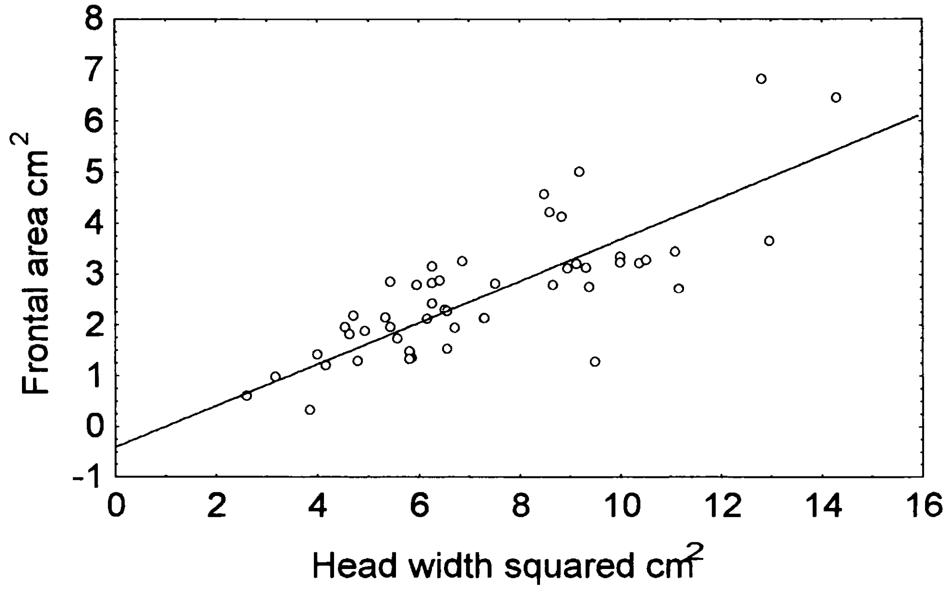


Figure 5-3, The relationship between head width and frontal area of *Ecdyonurus*.

5.4.2 Phototaxis

All the taxa tested except *Baetis rhodani* showed a strong preference for the shaded area, Table 5-3. The almost 50-50 response to either light or shade would indicate that *Baetis rhodani* has no preference. There was no significant difference in the weights of *B. rhodani* individuals which preferred shade to those that preferred light.

When the animals were exposed to the same conditions with moving water they all initially moved upstream into the shaded zone, including *B. rhodani*. However as velocity increased, they moved into the lit zone where they would still resist entrainment.

Table 5-3, Percentage of animals preferring the shaded area over the lit area.

	Taxa *Ecdyonurus*	*Baetis rhodani*	*Gammarus pulex*	*Asellus aquaticus*	Tipulidae
Mean Weight g	0.015	0.005	0.045	0.011	0.191
Standard deviation	0.009	0.003	0.062	0.006	0.088
n	20	19	20	20	20
Shade % of animals	90	52	95	85	80

5.4.3 Rheotaxis and swimming

Ecdyonurus

This species, like *B. rhodani,* swam in short bursts . The length of the bursts decreased with increasing velocity (personal observation only). It remained close to the substrate for the majority of the time but on occasion would swim further up into the water column. When velocity increased *B. rhodani* would either enter the drift or, if the water velocity was not sufficient to wash the animal out of the experimental channel, it would frequently alight on the floor and then enter the drift again. There was a marked decrease in an individual's upper velocity tolerance with repeated exposure making it impossible to use the same animal for two consecutive runs. This was only attempted if there had been a problem during the first run. On a number of occasions individuals would resist entrainment until the velocity was very high >1.5 ms^{-1}. When this occurred they assumed a flattened position with their body pressed closely to the floor. This posture was taken up as velocity increased although only infrequently did the animals persevere until velocities were very high (>1.5 ms^{-1}). On other occasions the animals would move to the flume edge as velocity increased, presumably gaining advantage from the reduced water velocity at these locations.

Baetis rhodani

When moving upstream or downstream, the animal swam in bursts coming back down onto the floor periodically. Above a certain velocity the animal would not swim downstream: instead it appeared to drift. After leaving the substrate it would move up through the water column rather than drift near the floor. It was not clear whether this action was voluntary or passive. Once in the water column the animal assumed a posture where its abdomen was arched upward and its cerci aimed forward over its head. After travelling in this manner the animal would float down through the water column and grasp the floor with its claws. If the animal had not travelled far enough (assuming the animal is making the decision about what distance to travel), while still suspended it would flick its abdomen when descending which stopped the descent and allowed further travel downstream. Some individuals would also move to the side of the flume where they could resist entrainment more easily. It was clear that an individual would choose whether or not to enter the drift, although there was always a point at which velocity was sufficiently high that they could no longer remain in contact with the substratum.

Gammarus pulex

Like the previous two taxa, this species showed a range of responses to high velocities. Unlike the other taxa, *G. pulex* would quickly move upstream once introduced into the flume. It also differed in its use of the whole water column while swimming, something only *B. rhodani* did as frequently. As velocity increased *G. pulex* would either get washed out of the experimental channel or alternatively would move down onto the flume floor. There it would hold on with its frontal appendages, from either thoracic or head sections, while facing upstream. This animal would frequently tilt its body upwards to the rear, from its point of anchorage, at an angle of as much as 45° or more. Depending on the individual and the exposure velocity, three related responses were observed. Firstly individuals would release their hold and drift downstream (after moving up into the water column), alternatively they would release and move downstream pushed by the flow, but would remain close to the floor and periodically re-attach and then get swept down again, sometimes simultaneously moving to the flume wall. Their capacity to perform this action was extraordinary; they could on occasion move at right angles to the direction of flow, although more normally there was some downstream drift involved also. This movement at right angles could occur even at quite high velocities.

Asellus aquaticus

Animal availability in the wild decreased shortly after the initial phototaxtic test and no behavioural observations could be made in running water.

Tipulidae

When moving upstream or against the current, the animals appeared to bite the substrate with their mandibles and while so anchored would draw their abdomen further forward. This activity was accompanied by moving the head from side to side. If the current proved too strong the animal would release its grip and roll downstream angling its body so it ended up at the flume wall. This process was completed in stages with the animal holding on, reorienting, and then releasing until it reached its destination. Once it reached the flume wall it expanded its body into the corner between floor and wall. Here velocity was not measurable, but was noticeably less than in the centre of the channel.

The increase in discharge necessary to dislodge a tipulid from this refuge was substantial. If the water velocity was too fast and the animal could not reach the flume edge it would release its grip and drift downstream, usually rolling over the flume bottom. Like the other taxa, Tipulidae that were repeatedly placed in the flume showed an increased readiness to drift and the velocity at which they drifted decreased over the duration of the experiment. One individual appeared to attach by means of silk thread, to the flume floor during high flow. This left the animal floating above the substrate (circa 1 cm) and gave it the capacity to remain in position at much higher velocities than other Tipulidae. Some Tipulidae do spin silk from labial glands although this capacity is limited to the aquatic and semi-aquatic forms, (G. Hancock, Glasgow University pers comm.).

5.4.4 Entrainment logistic curves

Tipulidae

There was no significant difference in the mean weight of the groups assigned to each velocity (ANOVA), see Table 5-4 and Figure 5-4. The change from active behaviour to either resistance to entrainment or to be actually entrained, occurred over a short velocity range (Figure 5-5). Few animals showed resistance behaviour and all were entrained when water velocity had reached 0.12 ms^{-1}.

Table 5-4 Tipulidae mean and standard deviation of weight for each experimental exposure to velocity, n = 5.

Exposure ms^{-1}	0	0.04	0.06	0.08	0.1	0.12
Mean g	0.230	0.202	0.152	0.189	0.160	0.221
Standard deviation	0.089	0.080	0.030	0.092	0.051	0.070

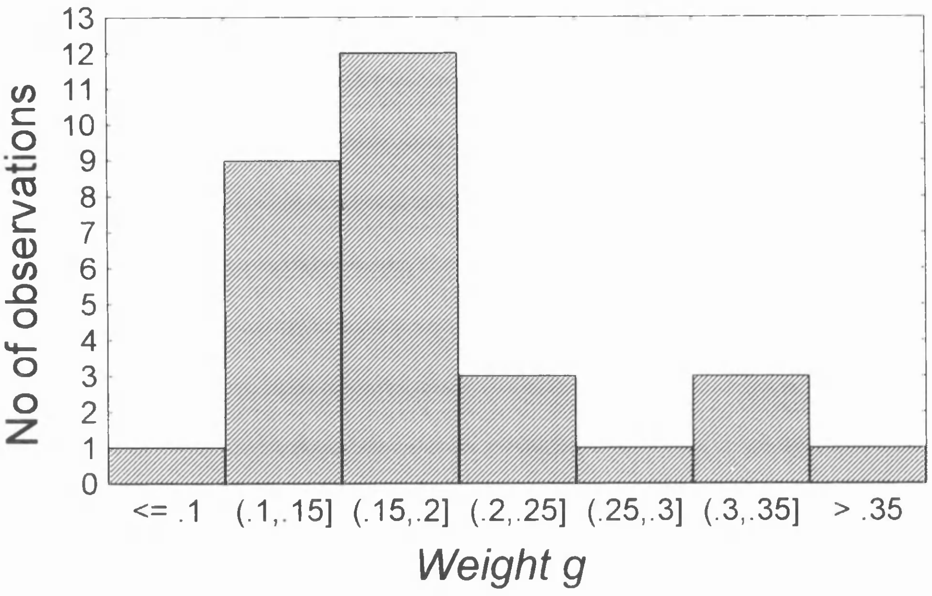


Figure 5-4, Weight distribution of Tipulidae used in logistic regression experiments.

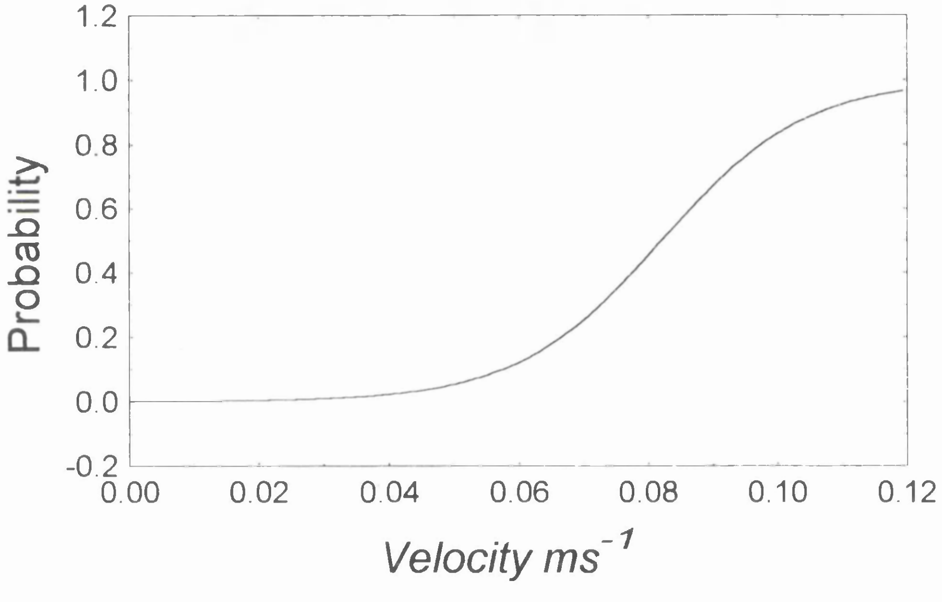


Figure 5-5, Logistic regression analysis of Tipulidae behaviour showing the probability of the animal exhibiting either resistance to entrainment or the animal actually being entrained. Equation of the line is $y = \exp(-7.35+(89.69)*x)/(1+\exp(-7.35+(89.69)*x))$, Chi square = 22.7, $p<0.0001$.

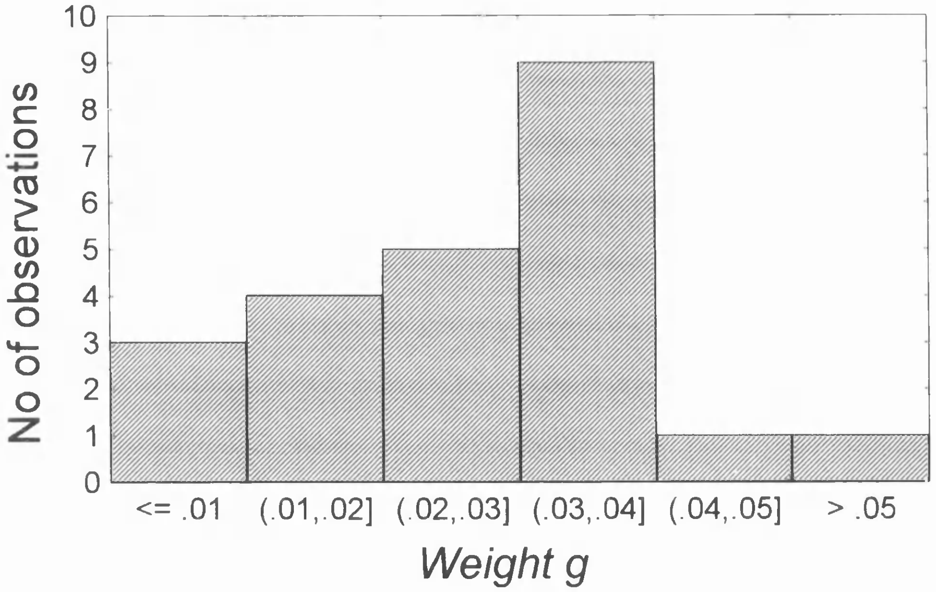


Figure 5-6, Weight distribution of *Gammarus pulex* used in logistic regression experiments.

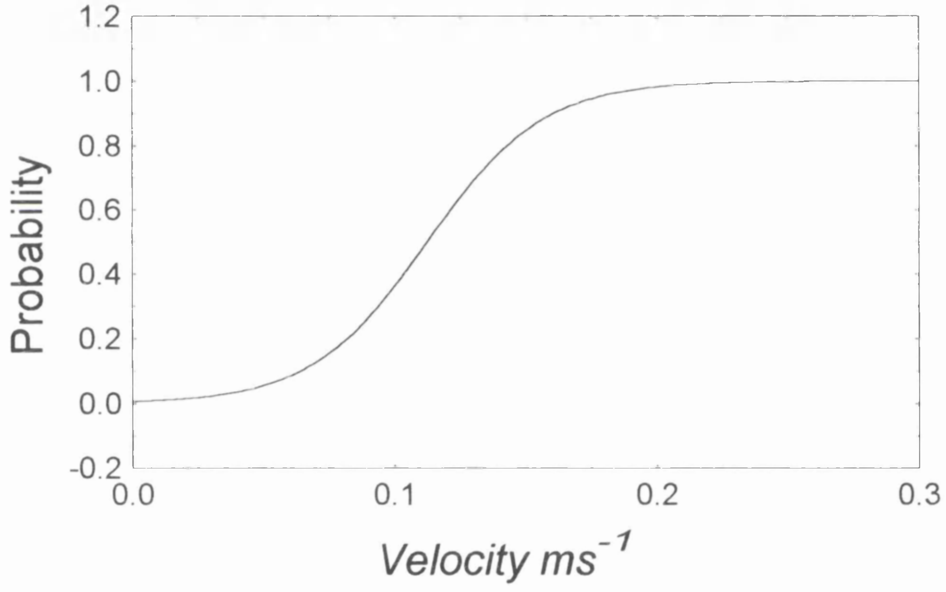


Figure 5-7, Logistic regression analysis of *Gammarus pulex* behaviour showing the probability of the animal exhibiting either resistance to entrainment or the animal actually being entrained. Equation of the line is $y = \exp(-5.12 + (45.6)*x)/(1+\exp(-5.12 + (45.6)*x))$, Chi - square = 20.58 ,$p<0.0001$.

Gammarus pulex

There was no significant difference in the weights of animals assigned to each exposure (ANOVA), see Table 5-5 and Figure 5-6. The range of responses to velocity was greater for *G. pulex* than for the Tipulidae, Figure 5-7.

Table 5-5, *Gammarus pulex* mean and standard deviation of weight for each experimental exposure to velocity.

Exposure ms^{-1}	0	0.1	0.15.	0.2	0.3
n	5	4	5	5	4
Mean g	0.027	0.029	0.023	0.027	0.027
Standard deviation	0.013	0.018	0.007	0.012	0.012

5.4.5 Effect of weight on entrainment of Tipulidae

All animals were entrained in a short band of velocities. There were significant positive correlations between weight and the lowest and highest velocity at which animals became entrained. One of the individuals used was very large (0.763 g) and considered an outlier. Removal of the outlier did not affect the significance of the relationship between velocity and the lower velocity of entrainment. The relationship between the highest velocity of entrainment and velocity did become non-significant on its removal.

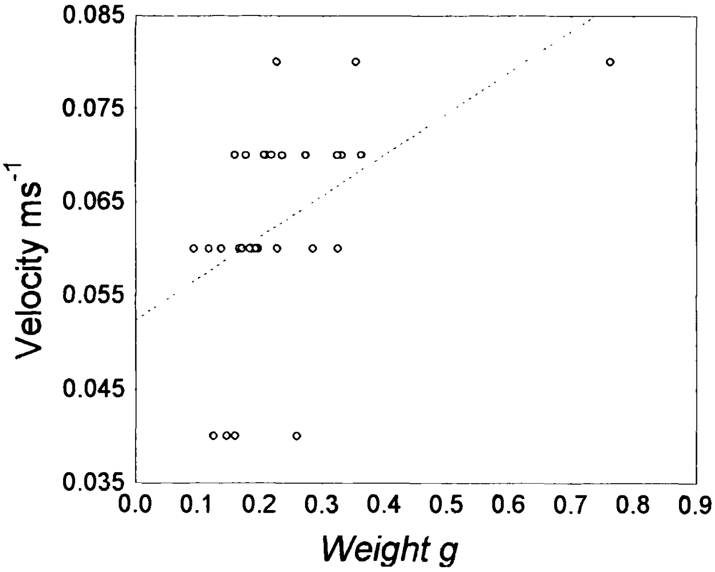


Figure 5-8, The lowest velocity of entrainment exhibited by the Tipulidae against body weight. Spearman rank correlation, R = 0.56, p<0.005, n= 29. Equation of the line; y = 0.052+0.044*x.

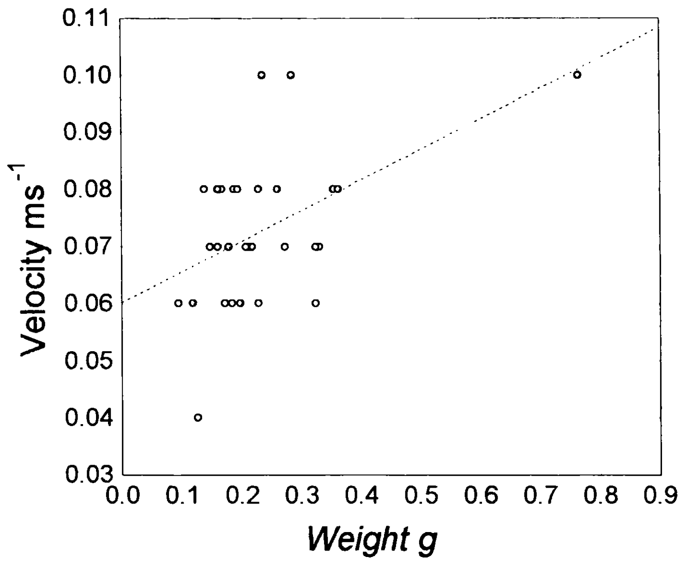


Figure 5-9, The highest velocity of entrainment exhibited by the Tipulidae against body weight. Spearman rank correlation, R = 0.40, p<0.05, n= 29. Equation of the line; y = 0.06+0.053*x.

5.5 Discussion

The observed responses of the benthic invertebrates are consistent with the hypothesis that animals frequently choose to enter the drift. Similar behaviour to that observed here has been interpreted as a reluctance to drift (Lancaster 1999) and this is not contradicted, rather it is suggested that a choice is being made and that the animals can become more willing to enter the drift if stressed. In none of the exposures made during the present study were the animals given any refugia. Their capacity to find the edge of the flume where velocity was low, highlights a highly developed rheosensory capability, across all taxa examined. This capacity together with the ability to alter the length of drift - by either rolling (tipulids) or flicking the body (*Baetis rhodani*) up into the water column - may help explain the capacity of invertebrates to choose substrate type directly from drifting (Walton Jr 1978).

The negative phototactic response of all subject animals, excluding *B. rhodani* supports the use of substrate as shelter. Where the river is not shaded by vegetation the substratum is the only place which is dark. By seeking such a location macroinvertebrates are choosing an area in which is presumably difficult for visual predators to operate. Areas which are dark are likely to be deep in the substrate matrix and should have lower shear stresses than substrate elements close to the bed surface, however the hyporheic refuge theory has only been supported in part by field experiments (Palmer *et al.* 1993b) but the question here is more concerned with animals sheltering not from serious floods but from 'normal' flow conditions. Animals in the substratum would require less energy to maintain position.

However both *G. pulex* and *E. ignita* have been shown to use woody debris as shelter when velocity is increased, although *G. pulex* made more efficient use of the refuge (Borchardt 1993). Although no light measurements were reported from amongst the woody debris it is clear from their size that they would have had some shaded areas.

From the evidence presented here it is possible that the two stimuli, both light and current could work in concert or independently. Further work which identifies which stimulus is dominant would give a possible insight into the relative importance of predator avoidance versus entrainment.

That no response to light was observed in *B. rhodani* also fits with our knowledge of the animal as a good swimmer and suggests that it is more flexible in its response to negative stimuli than the other taxa, e.g. predators. The situation is not simple though as both *B. rhodani* and heptageniids nymphs are known to seek shelter among the substrata; in this case it was suggested that they are avoiding predators (Huhta *et al.* 1995). *Baetis* species are known to show strong diel periodicity in drifting (Poff & Ward 1991; Tikkanen *et al.* 1994), but it is not clear if this is regulated by light levels or circadian rhythms. In this instance, if *B. rhodani* was shown to drift at night, the lack of preference for light or dark conditions would be indirect evidence for an internal clock. As drifting in *Baetis* can be very seasonal and local drift records are few so no direct conclusions on this subject can be made (Rincon & LobonCervia 1997), but the possibility for future work exists. [1]

The Tipulidae occur at higher velocities in the field than those at which they were entrained in the flume (see Chapter 4 Section 4.3). This could be for two reasons. Firstly the flume substrate afforded less grip than the substratum in the field, or, second, the animal remains below the surface of the river bed for the majority of the time. As the tipulids could withstand only very low velocities, lower than those expected near the river bed, they must avoid the substratum surface. This highlights the fact that these organisms are exploiting the habitat in very different ways and suggests that niche differentiation is occurring along these physical gradients.

The increased ability of larger Tipulidae to withstand entrainment is a situation observed in other taxa. For some Trichoptera it has been suggested, that because of this relationship the chances of accidental dislodgement decrease with size (Otto 1976). That the surface area to volume ratio of a small object is much greater than that of a similarly shaped large object is often quoted in texts on thermo-regulation. It is well established that the surface area to volume ratio of a small object is much greater than that of a similar shaped large object (Schmidt-Nielson 1990). If we assume that weight will increase in a linear manner with increasing volume, ignoring for the moment the stepped size increases exhibited by insect instars, then the ratio of frontal area to weight of a small tipulid will be relatively greater than that of a larger specimen. Therefore, there would be relatively less force exerted on a larger animal per unit weight. In theory, therefore, a larger animal would need to expend less energy to withstand entrainment. This should be applicable to other taxa also: the only limit

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[1] Some 24 hr drift samples were taken from the Blane Water but the sample size was small and the results inconclusive. Directly upstream of the drift nets was a very large population of Hydropsyche

would be the individual's height increase. As the animal's height increases it could project too high into the boundary layer subjecting the animal to relatively higher velocities. This would be dependent on the increase in velocity with depth which, in shallow riffles, can be steep. This would provide one explanation for the ability of large tipulids to withstand higher velocities since the relative increase in volume equates to increased muscle. Whether resistance is a physical act or passive inertia needs to be clarified. From the observations of the animals' behaviour it seems likely to be a combination of both.

The velocities at which the Tipulidae and *G. pulex* drifted will have been influenced by the substrate in the flume bottom. It seems likely that this type of work will increase where it is necessary to get exact measurements of the flow preferences of invertebrates. It would appear likely, therefore, that further studies of this type are required during which exact measurements of the flow preferences of different species of invertebrates could be made. Standard substrates would be used to allow comparisons with both field conditions and other experimental studies.

Giller & Malmquist (1998) have suggested that a pluralist approach to understanding community structure is necessary; it is no longer sufficient to only argue about the relative importance of biotic versus abiotic factors. Drift by benthic invertebrates appears to be a general response to both types of factors (Brittain & Eikeland 1988; Collier & Wakelin 1992; Kratz 1996). The data presented in this chapter add weight to the argument that individuals actively choose to drift and that this response is plastic at the level of the individual. Individual plasticity is therefore a useful measure of the relative importance of the various factors affecting community structure.

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larvae which could also have significantly altered the composition of the drift (Georgian & Thorp 1992).

The process of drifting is likely to reduce the fitness of the animal. By this I mean the actual drift itself not the process which is actually beneficial e.g. drifting from one food patch to another is consuming time which could be spent feeding, but the process may be necessary if food is to be found at all (Kohler 1985). So if the drifting behaviour of an animal is altered its fitness, as measured by fecundity, is likely to be altered too.

5.6 Conclusions

- Negative phototactic responses of benthic invertebrates agree with their known use of substrate as a shelter.
- Benthic invertebrates have strong rheosensory responses.
- Entrance into the drift is a matter of choice below certain upper velocity limits. These limits are species-specific.
- There is a positive relationship between body size and the capacity of a tipulid larvae to withstand entrainment.

Chapter 6: Invertebrate hydraulic microhabitat and community structure in *Callitriche stagnalis* Scop. patches

6.1 Introduction

When macrophytes are included in rehabilitation schemes for channelled rivers they can potentially provide a diverse habitat for invertebrates by interacting with local flow conditions (Marshall & Westlake 1990; Newbury & Gaboury 1993). For practical management purposes it is useful to know how much additional invertebrate diversity and biomass may be supported by utilising macrophytes as part of an individual river rehabilitation scheme, under specific flow conditions. I use the term diversity of invertebrates to encompass taxon richness, abundance and evenness (the relative number of individuals of each taxa). Previous work e.g. (Gregg & Rose 1982) has demonstrated the extent to which macrophytes can alter the stream flow microenvironment. Large-scale studies (e.g. Jenkins *et al.* 1984; Ormerod 1988) have demonstrated how this increased habitat diversity in turn influences the occurrence of invertebrate assemblages in vegetated and unvegetated parts of the river environment. Sand-Jensen & Mebus (1996) showed that a range of flow conditions were present in patches of the submerged macrophyte *Callitriche cophocarpa*. Other studies (Wright 1992); Jeppesen *et al.* (1984) found that invertebrate communities present in macrophyte patches (including *Callitriche*) could differ substantially from those occurring in unvegetated patches of river bed, having higher taxon richness, numerical abundance and specifically high numbers of Chironomidae and Simuliidae. Woody debris has been show to have increased species richness if its complexity is increased in streams, suggesting increased habitat complexity as the mechanism behind high species richness and abundance in plant patches too (O'Connor 1991).

The Blane Water is a small unregulated stream which supports a *Callitriche*-dominated macrophyte flora typical of many small British rivers in which rehabilitation schemes are being considered or implemented. The relationship between flow conditions and invertebrate community structure within different parts of submerged beds of *Callitriche stagnalis* Scop., and in adjacent unvegetated patches of river substrate in the Blane Water was investigated. The results are considered in relation to the value added to river rehabilitation schemes by the inclusion of macrophytes, in terms of increased invertebrate diversity support capacity.

The aims of the chapter are to show that different sections of *Callitriche instagnalis* support different assemblages of benthic invertebrates and that this may in part be related to the flow conditions in and around the plants. Specifically that the outside of the plants is an extreme environment for benthic invertebrate suitable for a limited number of specialist taxa only.

6.2 Methods

6.2.1 Source of Plants

Plants and substrate were collected from riffle sections of the Blane Water, a gravel bed river, at Blane Bridge (UK National Grid reference NS507852) in Scotland during June 1998. The site is down stream from a trout fishery and is classified as organically enriched by the Scottish Environmental Protection Agency, although water quality is classified as high (Doughty & Maitland 1994). The only noticeable effects of enrichment are higher numbers of chironomids and annelids than would otherwise be expected. Channel width in the sampling area ranged from 8-13 m, depth from 7-22 cm and velocity from 0 to 0.35 ms^{-1}.

6.2.2 Measurements

Ten *Callitriche stagnalis* stands were chosen at random within a c.100 m stretch of river. Water velocity and depth were measured in front, above, in the middle and at the bottom of each stand using an electromagnetic velocity meter (SENSA). At the mid channel side of each plant, velocity and depth were measured and substrate type was visually estimated (% scale) using the following particle size scale: sand (0.06 mm-2 mm nominal diameter), fine gravel (2-10 mm), gravel (10-64 mm) and cobble (64-256 mm). A reference scale was carried in the field to confirm particle size when necessary. Mean water column velocity measurements taken outwith the stands were measured at 0.4 depth from the river bed (Smith 1975) as 50 second averages.

The total area of bed occupied by each stand was estimated using a quadrat with 25 cm^2 squares. Invertebrate samples were taken separately from the outer, middle and root sections of the plants by placing a net downstream and trimming the desired section of the stand with scissors and letting it float into the net. Sections were defined using stand length and depth as follows; outer = outer 20%, mid = all other material above substrate, root = material within the bed. When removing the roots all the substrate which had been underneath the stand was disturbed and the invertebrates collected into the net placed downstream. A Surber sample was then taken from the mid channel point where substrate type had been assessed, 10 surber samples in total. I estimated the near bed velocities at the Surber samples by using values which were 10% of those at 0.4 depth from bed, as suggested by Carling (1992).These samples, and the sections of stands, were immediately placed in 70% alcohol to preserve the invertebrates. All samples were sorted on white trays and animals identified to the following taxonomic levels: Annelida to subclass; Diptera to family or genus and all other taxa to genus or species. Other studies show larvae and adults of Coleoptera have differing hydraulic habitat preferences (Degani *et al.* 1993) and so are treated separately here.

6.2.3 Data manipulation

To compare densities of invertebrates between stand sections, abundance values were standardised to estimated wet weight of stands. Because of the necessity of immediately preserving invertebrate samples in alcohol, in the field, the plant material in the samples could only be weighed after a storage period in 70% alcohol. It was necessary to see if samples of different weights were affected equally. The relationship between dry weight post storage with wet weight prior to storage was linear for log-log data as determined by regressing the wet weight of 24 control stand samples against their dry weight.

$$\text{LnWet weight} = 2.59+0.92(\text{Ln Dry weight}), \quad (R^2 = 0.978)$$

This equation was used to transform dry weight values to wet weight for the experimental plants.

6.2.4 Statistical analysis

Where direct comparisons between samples were made the Wilcoxon Matched-Pairs Signed-Ranks Test was used, which allows comparison between related samples (Sidney 1956). As either different sections of stands are compared or stands and adjacent sections of substrate (Surber samples) it was considered that they represented related, non-independent samples and that this test was the most applicable. Benthic invertebrates can have clumped distributions and it is possible that this could occur around some of the *Callitriche* stands; see Elliot (1977) for a comprehensive assessment of the possible spatial dispersions of benthic invertebrates. It was believed this could further influence the relatedness of spatially close samples and enhanced the applicability of the Wilcoxon Matched-Pairs Signed-Ranks Test

6.3 Results

6.3.1 Taxa abundance and richness compared between plant and surber samples

Although composed of many individual plant fronds, all stands had a similar growth form, being wider at the upstream end and tapering downstream, similar to a classic streamlined strut as described by Vogel (1994) but wider at the upstream end and generally more ragged. The area of stream bed occupied by stands was on average 467cm^2 (s.d.+/- 290cm^2). Substrate in the Surber samples was dominated by gravel (% composition of gravel always >90%). The substrate underneath the *Callitriche stagnalis* stands was mainly sand (% composition of sand always > 80%). *Callitriche* stands had higher, and significantly different total taxa abundance (no. of individuals of all taxa) and taxa richness than neighbouring substrate samples (Wilcoxon Matched-Pairs test $p<0.01$, $N=10$. Values standardised for sample area: the area of bed occupied by each stand. P value is for both cases, see Table 6-1 for abundance and richness data per sample). A list of taxa occurring in the Surber samples and plant stands is given in Table 6-2 with abundance (no. of individuals per sample) and frequency of occurrence (no. of samples a taxon occurs in).

6.3.2 Taxa abundance and richness compared between plant sections

Taxa richness was significantly different between outer and root sections of the stands. From the box plot in Figure 6-1 it is clear that the outer section supports the lowest taxa richness. Total taxon abundance was significantly different between outer and mid sections and outer and root sections. The box plot shows that the outer section of the stand supported the greatest abundance, see Figure 6-2, Table 6-1 for abundance and richness data per sample.

Table 6-1. Total abundance, number of individuals of all taxa per sample and Taxon richness, the number of taxa per sample. Values for stand sections (outer, mid, root) are standardised by weight of plant material in each section (no. of individuals per g wet weight of plant material). Values for whole stands are adjusted to the amount of river bed covered by a Surber sampler (no. of individuals per 625 cm^2 of river bed). In all cases n =10.

Sample	Abundance					No. of taxa				
	Outer	Mid	Roots	Stand	Surber	Outer	Mid	Roots	Stand	Surber
1	4.63	1.34	1.95	592	71	0.18	0.14	0.63	12	14
2	11.61	1.44	5.75	1650	135	0.39	0.22	2.03	14	16
3	3.50	1.54	1.78	488	87	0.18	0.13	0.47	19	11
4	10.49	2.54	1.39	578	94	0.14	0.41	0.38	15	14
5	2.97	2.07	2.63	486	134	0.17	0.12	0.49	15	17
6	6.01	1.51	0.90	388	94	0.25	0.15	0.23	19	12
7	5.31	2.22	0.87	213	53	0.13	0.07	0.14	13	16
8	3.12	2.56	1.19	422	97	0.07	0.33	0.27	13	15
9	1.96	5.02	2.00	979	54	0.32	0.76	0.49	18	13
10	1.29	1.81	1.99	546	90	0.14	0.24	0.49	15	16

Table 6-2. Taxa list of invertebrates occurring in *Callitriche stagnalis* stands and on unvegetated substrate; surber samples. Abundance values for stand sections are standardised by weight of plant material in each section (no. of individuals per g wet weight of plant material). Abundance values for whole stands and Surber samples are adjusted for the amount of river bed covered by the stand or Surber sampler (no. of individuals per cm^2 of river bed). All abundance figures are (means +/- standard deviation) x 10^{-3}. Number of occurrences is the number of samples a taxa occurs in. In all cases n =10.

Taxa	Abundance					No. of occurrences				
	Outer	Mid	Root	Stand	Surber	Outer	Mid	Root	Stand	Surber
Caenis rivulorum Eaton	1.3+/-2.9	0	1.3+/-2.9	3+/-5.5	0.1 +/- 0.4	2	1	2	3	1
Baetis rhodani (Pictet)	9.8+/-8.6	9.3+/-10.1	6+/-8.3	25.1+/-23.6	18.7 +/- 11.6	10	8	6	10	10
Ephemerella ignita (Poda)	26.7+/-14.6	54.4+/-17.7	28.2+/-13.3	109.2+/-24.9	13 +/- 8.1	10	10	10	10	9
Ecdyonurus	0.3+/-0.6	1.3+/-1.7	2.2+/-2.8	3.7+/-3	4.8 +/- 5.3	2	5	7	9	9
Rhithrogena semicolorata (Curtis)	0	0	0	0	0.2 +/- 0.5	0	0	0	0	2
Hydropsyche siltalai Döhler	0	1.7+/-4.4	0.3+/-0.7	2+/-4.4	1 +/- 1	0	2	2	4	7
Athripsodes sp.	0.3+/-0.8	0.3+/-0.8	2.5+/-5.8	3+/-6.4	0.7 +/- 1.5	1	1	2	2	2
Brachycentrus subnubilus Curtis	0.3+/-0.8	0.4+/-1.2	0	0.6+/-1.9	0.3 +/- 0.7	1	1	0	1	2
Odontocerum albicorne (Scopoli)	0	0	0.2+/-0.5	0.2+/-0.5	0	0	0	1	1	0

Taxa	Abundance					No. of occurrences				
Rhyacophila sp.	0.3+/-0.5	0.1+/-0.3	0.1+/-0.3	0.4+/-0.7	1.2 +/- 1.2	2	1	1	3	6
Glossosoma boltoni Curtis	0	0	0.1+/-0.3	0.1+/-0.3	1.7 +/- 3.1	0	0	1	1	5
Asellus aquaticus (L.)	0.5+/-1.3	4.8+/-7.5	1.1+/-1.5	6.4+/-9.7	0.5 +/- 0.8	2	7	5	8	4
Gammarus pulex (L.)	0.9+/-1.9	2.3+/-2.7	2.5+/-2.5	5.6+/-4.5	1.1 +/- 1.2	2	6	6	8	7
Ancylus fluviatilis Muller	0.5+/-1.6	0.2+/-0.4	1.4+/-3	2+/-3.1	1.9 +/- 3.6	1	1	2	4	4
Pisidium sp.	0	0.5+/-1.5	0.3+/-0.8	0.8+/-1.6	0	0	1	1	2	0
Limnius volckmari (Panzer) lar	0	0.5+/-0.8	3.8+/-4.1	4.2+/-4.1	2.2 +/- 2	0	3	9	9	9
Limnius volckmari (Panzer) ad	0.2+/-0.6	0.3+/-0.5	0.2+/-0.4	0.6+/-0.9	1.4 +/- 1.7	1	2	2	4	6
Elmis aenea (Muller) lar	0.2+/-0.4	0.8+/-1.4	4+/-5	4.9+/-6	1.2 +/- 1.7	2	3	8	8	5
Elmis aenea (Muller) ad	0.2+/-0.6	0	0.2+/-0.5	0.4+/-0.9	0.1 +/- 0.4	1	0	2	2	1
Oulimnius tuberculatus (Muller) lar	0.3+/-0.6	0.2+/-0.4	0.7+/-1.6	1.1+/-1.7	0.1 +/- 0.4	2	1	2	2	2
Oulimnius tuberculatus (Muller) ad	0	0	0.5+/-1.1	0.5+/-1.1	0.3 +/- 0.7	0	0	2	4	1

Taxa	Abundance					No. of occurrences				
Esolus parallelpipedus (Muller) ad	0	0	0.5+/-1.5	0.5+/-1.5	0.2 +/- 0.5	0	0	1	1	2
Oulimnius troglodytes (Gyllenhal) ad	0	0	0.2+/-0.4	0.2+/-0.4	0	0	0	1	1	0
Scirtidae	0	0	0	0	0.1 +/- 0.4	0	0	0	0	1
Leuctra fusca (L.) group	2.4+/-3.2	5.5+/-6.7	7.6+/-10.3	15.4+/-14.5	5.8 +/- 5.3	5	8	7	10	10
Capnia	0	0.1+/-0.3	0	0.1+/-0.3	0.2 +/- 0.7	0	1	0	1	1
Tipulinae	0	0	0.7+/-0.9	0.7+/-0.9	0.1 +/- 0.4	0	0	4	4	1
Limoniinae	0.1+/-0.3	0.2+/-0.4	4.8+/-5.4	5+/-5.4	1.9 +/- 2.1	1	1	9	9	6
Ceratopogonae		0.2+/-0.4	0	0.2+/-0.4	0	0	1	0	1	0
Simuliidae	291.7+/-351.4	24.3+/-35.5	1.8+/-4	317.8+/-370.7	8 +/- 13.9	10	6	3	10	7
Chironomidae	144.8+/-211.9	44.5+/-58.9	8.3+/-11.6	197.6+/-270.4	16.3 +/- 21.5	4	4	4	4	4
Hirudinae	0.3+/-0.8	1.3+/-1.8	9.3+/-10.3	10.8+/-11.5	2.6 +/- 0.7	1	5	9	9	10
Oligochaeta	0	0.1+/-0.3	15.8+/-31.9	15.9+/-31.8	5.2 +/- 2.7	0	1	8	8	10

6.3.3 Community structure

Samples taken from the outer, mid and root sections of the stands and surber samples were separated by Detrended Correspondence Analysis (DCA) (Jongman *et al.* 1987) using their macroinvertebrate communities, see Figure 6-3. Root section and Surber samples were not separated by the DCA, but 3 species did show a preference for the Surber samples over the root sections, see Table 6-3.

Table 6-3. Taxa with a significant preference for Surber samples over root sections (Wilcoxon matched pairs test, N = 10).

Taxon	z	P value
Baetis rhodani	2.80	0.01
Rhyacophila	2.20	0.05
Limnius volckmari	2.20	0.05

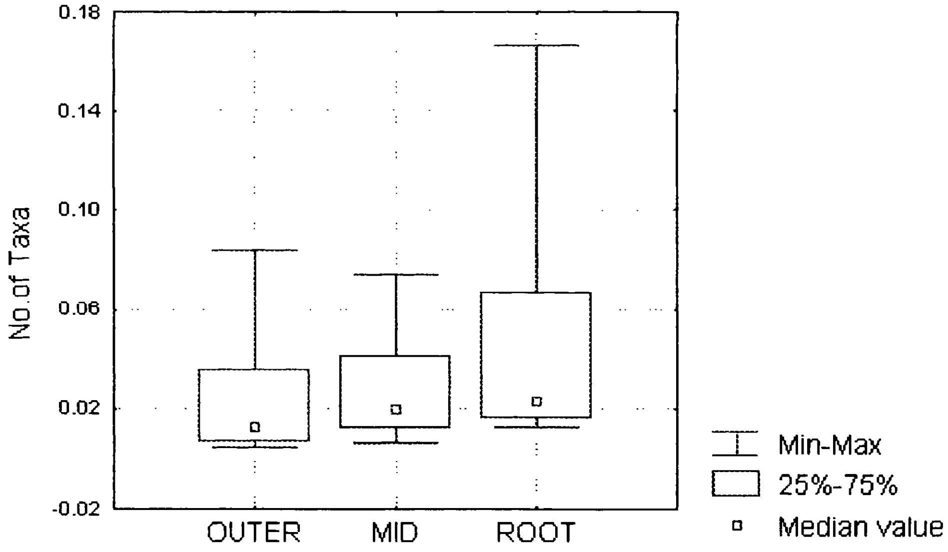

Figure 6-1 Number of invertebrate taxa no./g fresh weight. Outer was significantly different from root, Wilcoxon Matched-Pairs test: $p<0.05$, n=10. Values standardised for section weight.

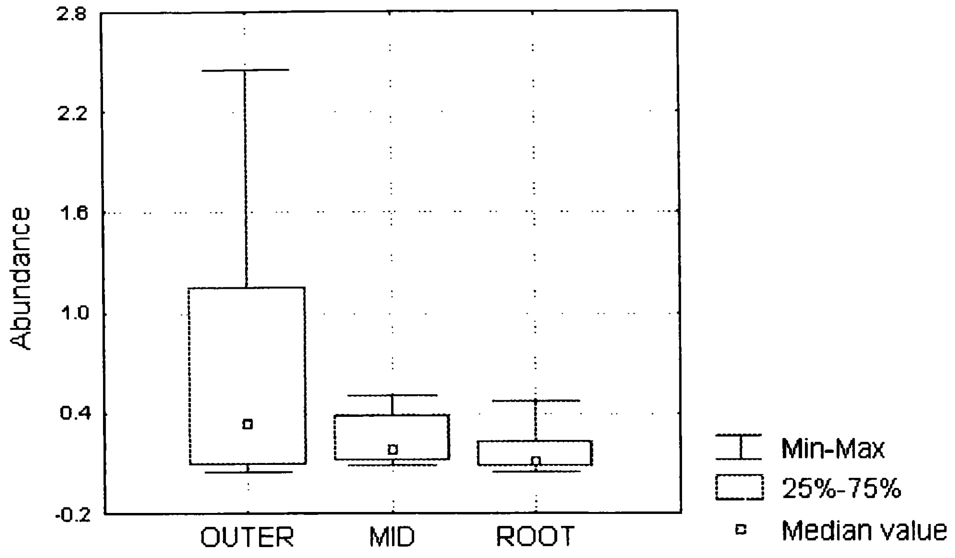

Figure 6-2 Relative abundance of invertebrates no./g fresh weight. Outer was significantly different from mid and root, Wilcoxon Matched-Pairs test: $p<0.05$, $n=10$. Values standardised for section weight.

To standardise between Surber and stand samples, sample area was used, but section weight was not taken into account. Other analyse showed that the same separation occurred if section weight was also used but separation of sites was not so clear. Samples from the outer section were most dissimilar to the Surber sample, the root section was most similar. The outer section was dominated by the filter feeding Simuliidae while in all other plant sections *Ephemerella ignita* dominates. In the Surber samples *Baetis rhodani* was the most abundant invertebrate. Community structure also differed between sections, see Figure 6-4. All three stand sections supported invertebrate communities which followed the broken stick model (Gray 1987). The outer section, which is exposed to the highest velocities, was the least equitable with the steepest gradient at the start and is the closest to a geometric series. Such a series is found in communities poor in species at the earliest successional stage after colonisation or when exposed to extreme conditions (Gray 1987). The **middle** section is more equitable and the root section is the most equitable having the largest

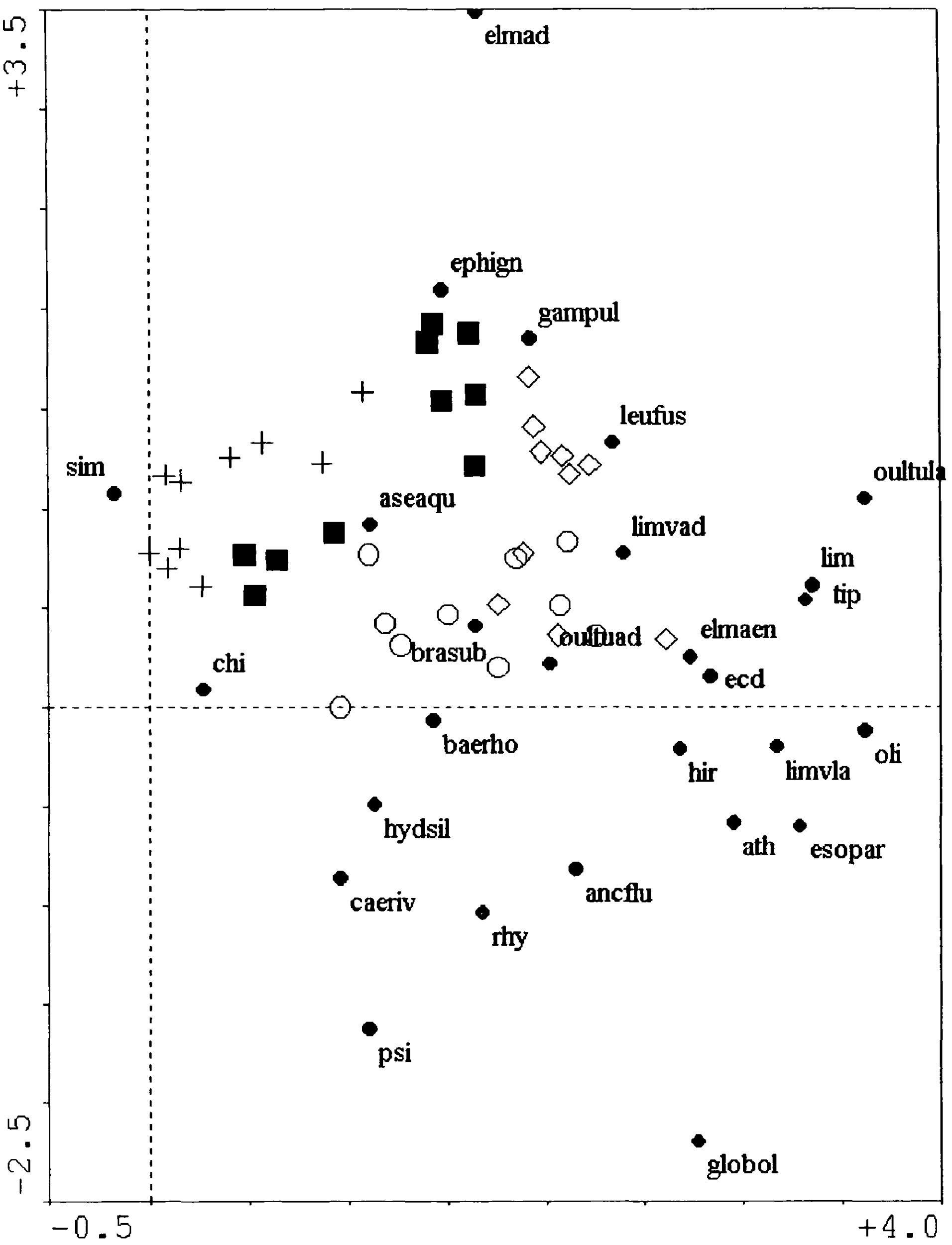

Figure 6-3 Detrended Correspondence Analysis Site by species biplot, (eigenvalues: axis 1 = 0.6, axis 2 = 0.136) Plant section and Surber symbols: Outer +, Mid ■, Root ◊ and Surber O. The location of each taxa is marked with ◆ and a taxa code. Taxa codes: *Caenis rivulorum* (caeriv), *Baetis rhodani* (baerho), *Ephemerella ignita* (ephign), *Ecdyonurus* (ecd), *Hydropsyche siltalai* (hydsil), *Athripsodes* (ath), *Brachycentrus subnubilus* (brasub), *Rhyacophila sp.* (rhy), *Glossosoma boltoni* (globol), *Asellus aquaticus* (aseaqu), *Gammarus pulex* (gampul), *Ancylus fluviatilis* (ancflu), *Pisidium sp.* (psi), *Limnius volckmari* larva (limvla), *Limnius volckmari* adult (limvad), *Elmis aenea* larva (elmaen), *Elmis aenea* adult (elmad), *Oulimnius tuberculatus* adult (oultuad), *Oulimnius* tuberculatus larva (oultula), *Esolus parallelpipedus* (esopar), *Leuctra fusca* group (leufus), Tipulinae (tip), Limoniinae (lim), Simulidae (sim), Chironomidae (chi), Hirudidae (hir), Oligochaeta (oli).

number of species which share the resource more evenly, in terms of producing individuals.

6.3.4 Prevalent flow conditions

It is suggested that stand structure and velocity combine to create a range of stability conditions, forming a series of microhabitats, in, on and outwith the plant beds. Velocity was significantly different and noted to be lower over the top of the stands than directly in front of the stands or in the adjacent Surber samples (Wilcoxon Matched Pairs $p<0.05$, $n = 10$). It is suggested that the shape of the stand is deflecting water to either side and creating flow conditions which are similar to sheet flow over the top of the stand; that is turbulent but uniform in direction of flow. The velocity at the top of the stand (0.25 ms^{-1}) was higher and significantly different (Wilcoxon Matched Pairs $p<0.05$, $n= 6$) than that in the middle (0.046 ms^{-1}) but velocity at the bottom (0.040m/s) of the stand was not significantly different from that in the middle. The near bed velocities at the Surber sample points (0.042 ms^{-1}), (estimated by adjusting velocity measured at 0.4 of depth from the bed) are not significantly different to those found in the mid and root sections of the stand. Estimates of near bed velocity over substrate were an order of magnitude lower than those measured on the outside of the plant stands. An estimate of the required velocity at 0.4 of depth above substrate flowing over unvegetated substrate that would produce a near bed velocity similar to the velocity experienced by the outer section of the stands would equate to 2.5ms^{-1}, or near spate condition, see Figure 6-5. This figure was derived from using Carling's (1992) estimate procedure in reverse starting with the flow over the outer section of the stands (0.25 m/s).

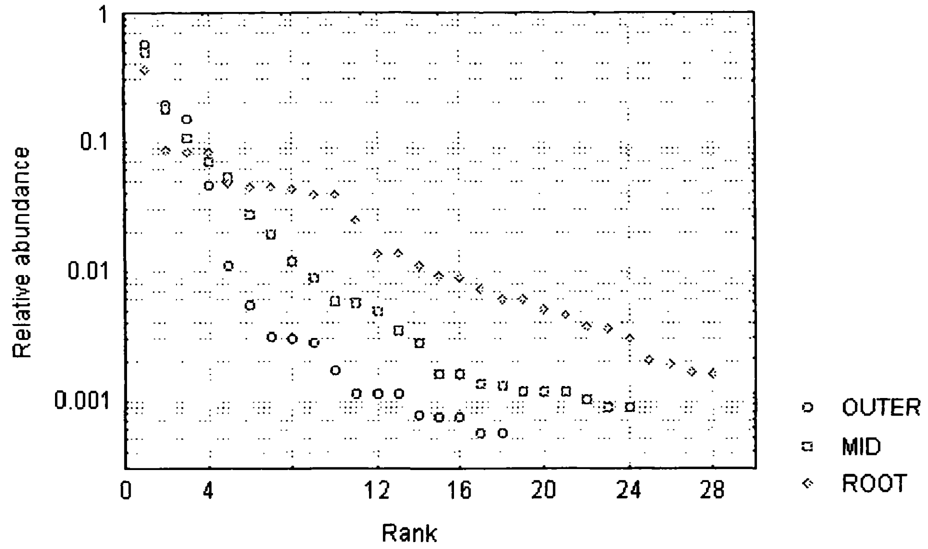

Figure 6-4 Rank abundance plot for the 3 plant sections. Relative abundance of invertebrates no/cm^2/g fresh weight.

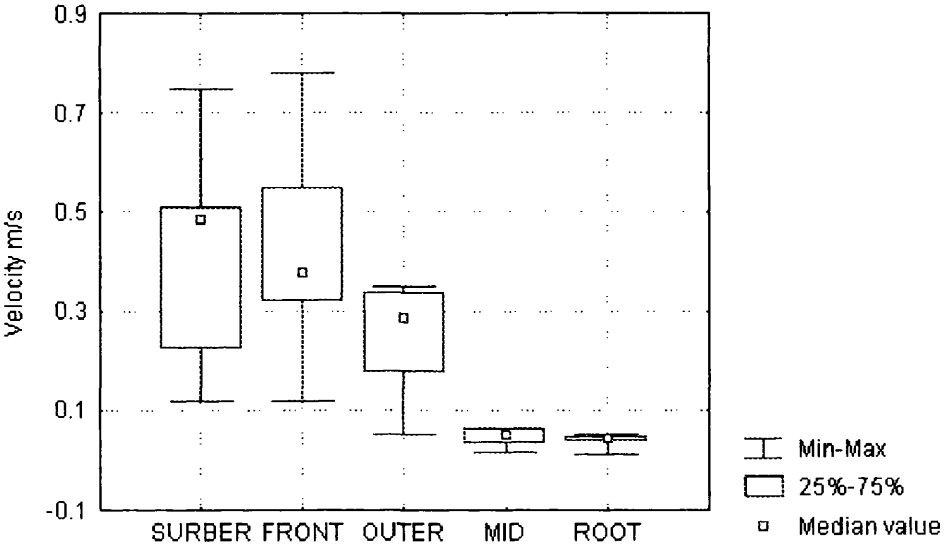

Figure 6-5 Velocity ms^{-1}, 50 second means.

6.4 Discussion

The presence of *Callitriche stagnalis* stands in the Blane Water increases the diversity of invertebrate habitat within the river. Taxa which occurred in the plant stands also occurred on the substrate, but some were present in higher numbers, on and within macrophyte beds. The stands extend the available substrate for invertebrate colonisation up through the water column, providing a continuum of conditions from high to low velocity. Adjacent benthic substrate does not provide the high velocities present on the outside of the plant stand in a sustained manner, that is only under near spate conditions would these high velocities be achieved. In addition the external surface of the stands greatly increases the area of high-flow substrate available for colonisation by invertebrates adapted to high flow conditions, especially Simuliidae (Hart & Latta 1986). Their habitat requirements include the need for fast flowing water through their labral fans but they avoid areas of maximum shear stress (Craig & Chance 1981; Lacoursiere 1991) and it is likely that the correct complex of hydraulic conditions are available on the surface of the plants.

Although taxon richness and abundance were not significantly different between the mid and root sections of the plants they were separable using DCA. The rank abundance plots demonstrated that the root section was more equitable than the mid section in resource distribution, hence the separation in the DCA biplot. This would suggest that conditions were more extreme in the mid section than the root section, which could be a product of longer term conditions than those measured in this study. The conditions present in these two sections allowed *E.ignita* to dominate where *B. rhodani* dominated in the Surber samples.

It has been suggested by (Sand-Jensen & Madsen 1992) that *Callitriche cophocarpa* "patches form a mutually protecting structure against high flows“ and “may, therefore... increase nutrient supply from sedimentation fine-grained particles". He later found that the sediment under stands often has high levels of organic matter (Sand-Jensen 1998) which could provide food for detritivores. In this study, despite finding that the substrate under our stands was more fine grained than that in unvegetated areas we found that no detrivore showed a preference for the root section, compared to the adjacent unvegetated sediment. I did not measure the amount of organic matter in the sediment.

The net result of the presence of the plants is to increase the invertebrate abundance and diversity present in the Blane Water. The assemblages present can be related to the structure of the stands, and how this influences the flow conditions experienced by the animals. The complexity of invertebrate community supported appears to be functionally related to position within the stand, with extreme conditions (on the external surface) supporting fewer species than within the bed. The total diversity supported is however a function of the total available set of conditions present in the river: on, in and between the stands.

From a management point of view it is clear that the presence of the stands substantially increases the invertebrate diversity and abundance supported by the river, particularly by increasing the habitat available for organisms (e.g. Simuliidae) which would otherwise find only a limited space for colonisation in their preferred high-flow conditions.

Callitriche stagnalis is a common species in British rivers, and elsewhere in Europe, with a high tolerance of disturbance (Sabbatini & Murphy 1996). Inclusion of transplanted material as part of rehabilitation schemes in the small gravel-bed rivers which are well-suited to this species would be likely to make a useful contribution to improving invertebrate support function of the river.

6.5 Conclusions

- The macrophyte stands supported a greater abundance of benthic macro-invertebrates than bare substrate.
- Higher velocities were recorded on the surface of the macrophyte stands than on the bare substrate.

- The invertebrate community occurring on the outside of the stands was dominated by Simuliidae and was less equitable than the community living on the interface between the plant stands and the substrate.
- By diversifying the habitat for benthic invertebrates, macrophyte stands are a potentially useful tool in river rehabilitation.

Chapter 7: General Discussion

7.1 Review of results

The original aim of this study was to provide data on flow preferences of benthic invertebrates which could contribute both to our ecological understanding of these organisms, and assist in construction of river management tools. In Chapter 2, I attempted to define deep and shallow river sections as riffles, pools and runs, using a range of criteria, and came to the conclusion that visual observation, coupled with depth and velocity measurements was necessary. Despite the minimal differences in benthic invertebrate community between the deep and shallow reaches of rivers used in this study it is likely that, indirectly at least, deep and shallow reaches do form important habitat units for the benthos. Predatory fish, salmonids, have a direct effect on the benthic community by catching animals drifting out of riffles into pools (Ade 1989); they also use riffle areas as spawning grounds. It has also been suggested that riffles provide more refugia and are less disturbed than pools (Scarsbrook & Townsend 1993).

In Chapter 3, I demonstrated both the relative homogeneity of the invertebrate community within each river, and also the existence of gradients between erosional and depositional conditions, with taxa occurring along these gradients: a situation found in similar studies in Australia (Barmuta 1989). The results of the analysis presented in Chapter 4 suggest that data collected using a randomised sampling strategy on instream habitat is not suitable for precise quantification of invertebrate flow preferences. The methods are sufficient to identify habitat preferences in a general manner - whether the animal prefers fast or slow conditions - but not quantitatively. This type of study does inform us of the relative importance of the environmental variables and how they interact with one another.

Laboratory flume experiments as carried out in Chapter 5 were also necessary to confirm findings made in the field. The approach taken in Chapter 5 allows for some measure of the plasticity in species responses to adverse flow conditions but does not offer a velocity gradient to the animals (which would be the most useful approach). The results also showed that the taxa had very different tolerance ranges for velocity and that behavioural control of drift may be possible. The final results chapter (Chapter 6) looked at a natural gradient of flow conditions in an aquatic macrophyte stand. The results presented in this chapter suggested that the higher velocities found on the outside of plant stands are not preferred by some species but were by others, e.g. *Simulium*. Whether this was due to velocity or some other another factor such as the presence of predators is difficult to elucidate from the present study and requires more work. Exposing the animals in a flume to a velocity gradient which covers the range found in the macrophyte patch under controlled conditions would go some way to testing the theory that water velocity preference is one of the main factors influencing benthic invertebrate occurrence.

7.2 Future Work

Identifying flow preferences of benthic invertebrates remains as a major aim necessary for the ecology and management of lotic freshwater systems. A refined version of the approach taken in this thesis could supply the information required.

A potential approach to elucidating the instream distribution of invertebrates involves both increasing and decreasing the spatial scale examined. To demonstrate clearer differences in invertebrate community structure one would need to examine a wider range of conditions e.g. in the rivers used in my study the deepest pool section was 1.5 m but a deeper range would be more informative, see Chapter 2, section 2.3. Large scale studies as suggested here have previously identified habitat units at the start of the study and based their sampling round these; edge, riffle, pool etc. A greater emphasis on covering wide ranges of parameters of interest, such as velocity, depth, substrate type and periphyton cover is an alternative approach advocated here. Reducing the scale of sample area and thereby making velocity measurements more accurate is also necessary and would seem sensible. Which spatial scale is correct for this type of procedure could be determined by a nested sampling design where the spatial scale is reduced at a number of levels. This type of study has been done at large physical scale, between rivers and reaches but not for instream habitat. Elliot (1977) gives a number of methods for determining whether benthic invertebrate distribution is aggregated or not and these could be applied to such data. It is likely that different taxa will exhibit clumping at different spatial scales and that a single taxon can also clump at different scales, e.g. in Chapter 2.3.6, p47, *B. rhodani* showed a preference for run sections in the Duneaton Water and Blane Water which is possibly caused by the presence of suitable, smaller habitat units: rocks with periphyton, which if examined at this scale the animals would also show a preference. This type of study could potentially use some of the new sampling methodology available such as stereo photography which allow fine scale measures of invertebrate distribution (Evans & Norris 1997). Direct measures of turbulence were not included in this study and it is proposed that any future work would include small scale localised measures of turbulence, which given the potential of turbulent water to surprise invertebrates and entrain them must mean areas of high turbulence are avoided. By turbulence here I do not simply mean non-laminar flow but gross, random motion of water at scales larger than the molecular.

By concentrating on individual species and recording their velocity and depth tolerances under controlled laboratory conditions we could begin to determine the importance of biotic and abiotic factors in their distribution. The lack of this type of basic knowledge hampers our interpretation of large survey work as carried out in this study. Based in the laboratory the work could proceed faster than trying to make accurate measurements of single species distributions in relation to velocity in the field, as suggested in the previous paragraph, which requires painstaking and time consuming methods, e.g. Hart et al. (1996). Field based measurements can only be applied to animals while they are on the surface of the substrate and, as many species spend large portions of time among the substrate matrix, a second series of experiments would be necessary to identify the proportion of time spent in both locations.

The spatial complexity of instream habitat has been linked to invertebrates' ability to withstand disturbance events (Lancaster & Hildrew 1993b). It is possible that streams of different retention capacity support invertebrates with different life history strategies. The homogeneity of instream habitat in channelled rivers could therefore cause the strategies of these organisms to be altered and could exert a selective pressure on the animals. The implications this has for the genetic variability or life history strategies of these animals has yet to be addressed. New work is required to look at this question which must incorporate studies of both juveniles and adults.

7.3 Management recommendations

This study aimed at a very specific question of river management: how to improve instream habitat for benthic macroinvertebrates. There are three major impacts on this habitat type in small Scottish streams; river channelisation and alteration of channel discharge either by damming, changes in catchment land use or water abstraction, often for fish farms. Management solutions applied in Scotland include the maintenance of minimum discharges (Q90 and Q95) from reservoirs and in streams from which water is abstracted, as imposed by SEPA (Marsden, M., SEPA pers comm) and the physical rehabilitation of channelised systems (Gilvear & Bradley 1997).

To date management guidelines suggested by public bodies (SNH and SEPA) and Non Governmental Bodies (e.g. RSPB) have mainly concentrated on physical habitat improvement for taxa other than macroinvertebrates, usually fish, birds and vegetation (Hoey *et al.* 1998). With the forthcoming EU Water Framework Directive which emphasises the ecological and physical naturalness of surface waters there will be a growing need to improve instream rehabilitation for invertebrates.

The importance of aquatic macrophytes as a useful tool in the conservation of macroinvertebrates has been previously highlighted (Wright *et al.* 1995). The results of Chapter 6 emphases this fact and illustrate the need for more basic research in this area if we are to manage aquatic vegetation for the benefit of macroinvertebrates without compromising the capacity of channels to deal with high flows; a problem which has a number of potential solutions (Fox & Murphy 1990a; Fox & Murphy 1990b). The density of macrophytes can even be incorporated into PHABSIM models if one wished (Hearne *et al.* 1994)! If used correctly macrophytes could potential mitigate the impacts of disturbance caused by rising discharge in a similar manner to woody debris (Borchardt 1993) and potentially increase the number of macrophyte species too (Hey *et al.* 1994).

Structural rehabilitation schemes are usually very successful in improving the diversity and productivity of the altered reaches (Swales & O'Hara 1980). The process of community alteration resulting from structural alterations to channels as part of habitat enhancement schemes can be difficult to judge in detail (Lynch & Murray 1994). If we wish to advance the science of this process and its usefulness as a management tool studies such a those advocated in section 7.2 will be necessary to improve their design.

PHABSIM is one of the few models which is now used to predict the amount of useable habitat for invertebrates at different discharges. In Chapters 3 and 4 I identified a number of problems with the data on which this model is based which need to be addressed if the model is to more accurately predict useable habitat for invertebrates. The previous section on further research suggests the type of projects necessary to collect this data.

There is a more fundamental problem associated with using this type of model and that is that its aim is only to make sure there is suitable habitat available for the animals. It does not take into account the dynamic nature of lotic systems which fuel the natural evolution of the invertebrate community e.g. it is quite possible for the same Q90 to be realised daily without variation. As ecologists our advice to managers should be to keep the physical system as natural as possible and the invertebrates will adapt to it. For the present it may be more suitable to use models based on historical flows or the flows implied by the rivers geomorphology, (see Jowett (1997) for a review of approaches). Geomorphologists have a more developed understanding of how any particular river should look and act than ecologists have of how animals interact with the habitat provided by the river (Werritty *et al.* 1994). Given the present state of knowledge in both disciplines ecologists should support the work of managers where they try and recreate the natural geomorphology of rivers.

Frequently this approach is too simplistic as it can be impossible to recreate a river's 'natural' geomorphology given the small sections of rivers that can be worked on and the numerous impacts presently outwith the control of managers, e.g. climate change and catchment land use (Langan *et al.* 1997). There is also the possibility that by increasing flow variability one could decrease available benthic invertebrate habitat (Englund & Malmquist 1996). This emphasises the need for an improved understanding of the interaction between benthic invertebrates and the physical habitat of rivers is necessary.

The approach taken in this thesis utilised a direct assessment of the habitat usage by invertebrate organisms: to develop suitable management models indirect interactions also need to be understood. The key to this understanding is the role of natural disturbance (flood events), interactions with riparian ecotones and instream habitat patchiness. Recent research which has started to describe the mechanisms underpinning these interactions was discussed at the start of this thesis (Chapter 1, section 1.1): it appears that much more work is required in this field.

Recent papers on the state of freshwater ecology and the management of freshwaters emphasises the need for ecologists to champion the relevance of their work and to review the paradigms of aquatic ecology (Reynolds 1998). This work also emphasises the need for 'quantitative bench marks and empiricised strategies *to be* set'. Reynolds (1998), similar to the approach take in the restoration of the Danube fish populations, (Keckeis & Schiemer 1992; Schiemer & Wieser 1992; Tockner & Schiemer 1997). This promotion of systems ecology has been heeded by UNESCO which now has a work program which is developing the tools and the paradigm of 'Ecohydrology'. Among the many UNESCO projects are those that look at the interactions of river flow instream and in the wider context of the catchment.

In summary the advice given to managers of aquatic ecosystems is not new and is that more basic scientific research is needed (Welcomme 1992). That UNESCO considers an ecologically balanced and soft engineering approaches to river management of importance emphasises the need for both more research and sensitive management.

References

Adams, C. E. & Maitland, P. S. 1998 The ruffe population of Loch Lomond, Scotland: Its introduction, population expansion, and interaction with native species. *Journal of Great Lakes Research* **24**, 249-262.

Ade, R. 1989 *The Trout and Salmon Handbook.* A Guide to the Wild Fish. Bromley: Christopher Helm Ltd.

Ambuhl, H. 1959 Die Bedeutung der Stromung als okologischer Faktor. *Schweiz Z. Hydrol* **21**, 133-264.

Armitage, P. D. 1976 A quantitative study of the invertebrates of the River Tees below Cow Green Reservoir. *Freshwater Biology* **6**, 229-240.

Armitage, P. D. 1995 Faunal community change in response to flow manipulation. In *The Ecological Basis of River Management* (ed. D. M. Harper & A. J. D. Ferguson), pp. 59-78. Chichester: John Wiley & Sons.

Armitage, P. D., Cranston, P. S. & Pinder, L. V. C. 1995 *The Chironomidae : Biology and Ecology of Non-biting Midges.* London: Chapman and Hall.

Armitage, P. D. & Gunn, R. J. M. 1996 Differential response of benthos to natural and anthropogenic disturbances in 3 lowland streams. *Internationale Revue Der Gesamten Hydrobiologie* **81**, 161-181.

Armour, C. L. & Taylor, J. G. 1991 Evaluation of the instream flow incremental methodology by United-States fish and wildlife service field users. *Fisheries* **16**, 36-43.

Bacher, I. & Waringer, J. A. 1996 Hydraulic microdistribution of cased caddis larvae in an Austrian mountain brook. *Internationale Revue Der Gesamten Hydrobiologie* **81**, 541-554.

Badcock, R. M. 1976 The distribution of the Hydropsychidae in Great Britain. In *Proceedings of the First International symposium on Trichoptera* (ed. H. Malicky). The Hague.

Barmuta, L. A. 1989 Habitat patchiness and macrobenthic community structure in an upland stream in temperate Victoria, Australia. *Freshwater Biology* **21**, 223-236.

Begon, M., Harper, J. L. & Townsend, C. R. 1996 *Ecology: Individuals, Populations and Communities.* Oxford: Blackwell Science.

Biron, P. M., Lane, S. N., Roy, A. G., Bradbrook, K. F. & Richards, K. S. 1998 Sensitivity of bed shear stress estimated from vertical velocity profiles: The problem of sampling resolution. *Earth Surface Processes and Landforms* **23**, 133-139.

Borchardt, D. 1993 Effects of flow and refugia on drift loss of benthic macroinvertebrates - Implications for habitat restoration in lowland streams. *Freshwater Biology* **29**, 221-227.

Borchardt, D. & Statzner, B. 1990 Ecological impact of urban stormwater runoff studied in experimental flumes - population loss by drift and availability of refugial space. *Aquatic Sciences* **52**. 299-314.

Bouckaert, F. W. & Davis, J. 1998 Microflow regimes and the distribution of macroinvertebrates around stream boulders. *Freshwater Biology* **40**, 77-86.

Boulton, A. J., Peterson, C. G., Grimm, N. B. & Fisher, S. G. 1992 Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* **73**, 2192-2207.

Bournaud, M. 1963 Le courant, facteur écologique et éthologique de la vie aquatique. *Hydrobiologia* **21**, 125-65.

Bovee, K. D. 1982 A guide to stream habitat analysis using instream flow incremental methodology. *United States Fish and Wildlife Service, Cooperative Instream Flow Group, Instream Flow information paper* **12**, 248.

Briggs, J. C. 1948 The quantitative effects of a dam upon bottom fauna of a small Californian stream. *Transactions of the American Fisheries Society* **78**, 70-81.

Brinkhurst, R. O. 1963 *A Guide for the Identification of British Aquatic Oligochaeta.* Scientific Publication No. 22: Freshwater Biological Association.

Brittain, J. E. & Eikeland, T. J. 1988 Invertebrate Drift - A Review. *Hydrobiologia* **166**, 77-93.

Brooks, S. S. & Boulton, A. J. 1991 Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbances in an Australian temporary stream. *Australian Journal of Marine and Freshwater Research* **42**, 295-308.

Brown, A. V. & Brussock, P. P. 1991 Comparisons of Benthic Invertebrates Between Riffles and Pools. *Hydrobiologia* **220**, 99-108.

Brown, H. P. 1987 Biology of riffle beetles. *Annual Review of Entomology* **32**, 253-273.

Brusca, R. C. & Brusca, G. J. 1990 *Invertebrates.* Sunderland, Massachuscetts: Sinauer Associates, Inc.

Buchan, L. A. J. & Padilla, D. K. 1999 Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecological Applications* **9**, 254-265.

Buffagni, A., Crosa, G. & Marchetti, R. 1995 Size-related shifts in the physical habitat of 2 mayfly species (Ephemeroptera). *Freshwater Biology* **34**, 297-302.

Carling. 1992 The nature of the fluid-boundary layer and the selection of parameters for benthic ecology. *Freshwater Biology* **28**, 273-284.

Carling, P. 1995 Implications of sediment transport for instream flow modelling of aquatic habitat. In *The ecological basis for river management* (ed. D. Harper & A. J. D. Ferguson). Chichester: John Wiley & Sons.

Carling, P. A. 1993 The nature of the fluid boundary layer and the selection of parameters for benthic ecology: Reply to Lamouroux. *Freshwater Biology* **30**, 333-335.

Ciborowski, J. J. H. 1983 Influence of current velocity, density, and detritus on drift of 2 mayfly species (Ephemeroptera). *Canadian Journal of Zoology* **61**, 119-125.

Ciborowski, J. J. H. 1987 Dynamics of drift and microdistribution of 2 mayfly populations - a predictive model. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 832-845.

Clausen, B. & Biggs, B. J. F. 1997 Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology* **38**, 327-342.

Clegg, J. 1952 *The Freshwater Life of the British Isles.* London and New York: Fredrick Warne &Co., Ltd.

Clifford, N. J. 1993 Formation of riffle pool sequences - field evidence for an autogenetic process. *Sedimentary Geology* **85**, 39-51.

Cobb, D. G., Galloway, T. D. & Flannagan, J. F. 1992 Effects of discharge and substrate stability on density and species composition of stream insects. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1788-1795.

Collier, K. J., Croker, G. F., Hickey, C. W., Quinn, J. M. & Smith, B. S. 1995 Effects of hydraulic conditions and larval size on the microdistribution of Hydrobiosidae (Trichoptera) in two New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **29**, 439-451.

Collier, K. J. & Wakelin, M. D. 1992 Drift of aquatic macroinvertebrate larvae in Manganuiateao River, Central North Island, New Zealand. *New Zealand Natural Sciences* **19**, 15-26.

Cowan, C. A. & Peckarsky, B. L. 1990 Feeding by a lotic mayfly grazer as quantified by gut fluorescence. *Journal of the North American Benthological Society* **9**, 368-378.

Craig, D. A. & Chance, M. M. 1981 Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydrodynamics. *Canadian Journal of Zoology* **60**, 712-724.

Crawley, M. J. 1986 *Plant Ecology*. Oxford: Blackwell Scientific Publications.

Crowl, T. A. & Schnell, G. D. 1990 Factors determining population-density and size distribution of a fresh-water snail in streams - effects of spatial scale. *Oikos* **59**, 359-367.

Crowl, T. A., Townsend, C. R., Bouwes, N. & Thomas, H. 1997 Scales and causes of patchiness in stream invertebrate assemblages: Top-down predator effects? *Journal of the North American Benthological Society* **16**, 277-285.

Cudney, M. D. & Wallace, J. B. 1980 Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern stream. *Holartic Ecology* **3**, 169-182.

Cummins, K. W. 1973 Trophic relations of aquatic insects. *Annual review of entomology* **18**, 183-206.

Dahl, J. & Greenberg, L. 1996 Effects of habitat structure on habitat use by *Gammarus pulex* in artificial streams. *Freshwater Biology* **36**, 487-495.

Davis, J. A. & Barmuta, L. A. 1989 An ecologically useful classification of mean and near -bed flows in streams and rivers. *Freshwater Biology* **21**, 271-278.

Death, R. G. 1996 The effect of patch disturbance on stream invertebrate community structure - the influence of disturbance history. *Oecologia* **108**, 567-576.

Death, R. G. & Winterbourn, M. J. 1995 Diversity patterns in stream benthic invertebrate communities - the influence of habitat stability. *Ecology* **76**, 1446-1460.

Degani, G., Herbst, G. N., Ortal, R., Bromley, H. J., Levanon, D., Netzer, Y., Harari, N. & Glazman, H. 1993 Relationship between current velocity, depth and the invertebrate community in a stable river system. *Hydrobiologia* **263**, 163-172.

Dejalon, D. G. & Sanchez, P. 1994 Downstream effects of a new hydropower impoundment on macrophyte, macroinvertebrate and fish communities. *Regulated Rivers: Research & Management* **9**, 253-261.

Dick, J. T. A. 1992 The nature and implications of differential predation between *Gammarus-pulex* and *G duebeni-celticus* (Crustacea, Amphipoda). *Journal of Zoology* **227**, 171-183.

Dick, J. T. A., Faloon, S. E. & Elwood, R. W. 1998 Active brood care in an amphipod: influences of embryonic development, temperature and oxygen. *Animal Behaviour* **56**, 663-672.

Dick, J. T. A., Irvine, D. E. & Elwood, R. W. 1990 Differential predation by males on molted females may explain the competitive displacement of *Gammarus-duebeni* by *G-pulex* (Amphipoda). *Behavioral Ecology and Sociobiology* **26**, 41-45.

Dick, J. T. A., Nelson, N. & Bishop, J. D. D. 1997 Introduction experiments with *Gammarus* spp. (Crustacea: Amphipoda) in the Isle of Man (British Isles), 1949-1995. *Journal of Zoology* **242**, 209-216.

Dingman, S. L. 1984 *Fluvial Hydrology*. New York: Freeman and Company.

Dittmar, H. 1955 Ein Sauerlandbach. Untersuchungen an einem Wiesen-Mittel-gebirgsbach. *Arch. Hydrobiol.* **50**, 305-552.

Dodds, G. S. & Hisaw, F. L. 1924 Ecological studies of aquatic insects. I. Adaptation of mayfly nymphs to swift streams. *Ecology* **5**, 137-148.

Dodds, G. S. & Hisaw, F. L. 1925 Ecological studies of aquatic insects. III. Adaptation of caddisfly larvae to swift streams. *Ecology* **6**, 123-137.

Dorier, A. & Vaillant, F. 1955 Sur le facteur vitesse du courant. *Verh. int. Verein. theor. angew. Limnol.* **12**, 593-597.

Doughty, C. R. & Maitland, P. S. 1994 The ecology of the River Endrick: present status and changes since 1960. *Hydrobiologia* **290**, 131-151.

Downes, B. J. & Jordan, J. 1993 Effects of stone topography on abundance of net-building caddisfly larvae and arthropod diversity in an upland stream. *Hydrobiologia* **252**, 163-174.

Downes, B. J., Lake, P. S. & Schreiber, E. S. G. 1995 Habitat structure and invertebrate assemblages on stream stones: A multivariate view from the riffle. *Australian Journal of Ecology* **20**, 502-514.

Dudgeon, D. 1991 An experimental-study of abiotic disturbance effects on community structure and function in a tropical stream. *Archiv Fur Hydrobiologie* **122**, 403-420.

Dudgeon, D. 1993 The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshwater Biology* **30**, 189-197.

Dudgeon, D. & Chan, I. K. K. 1992 An experimental-study of the influence of periphytic algae on invertebrate abundance in a Hong-Kong stream. *Freshwater Biology* **27**, 53-63.

Ebrahimnezhad, M. & Harper, D. M. 1997 The biological effectiveness of artificial riffles in river rehabilitation. *Aquatic Conservation-Marine and Freshwater Ecosystems* 7, 187-197.

Egglishaw, H. J. & Mackay, D. W. 1966 A survey of the bottom fauna of streams in the Scottish highlands. Pt. III. Seasonal changes in the fauna of three streams. *Hydrobiologia* **30**, 305-334.

Egglishaw, H. J. & Morgan, N. C. 1965 A survey of the bottom fauna of streams in the Scottish highlands. Pt. II. The relationships of the fauna to the chemical and geological conditions. *Hydrobiologia* **26**, 173-183.

Elliot, J. M. 1977 *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates*. Windemere: Freshwater Biological Association.

Elliot, J. M. & Mann, K. H. 1979 *A Key to the British Freshwater Leeches with Notes on their Life Cycles and Ecology*: Freshwater Biological Association.

Englund, G. & Malmquist, B. 1996 Effects of flow regulation, habitat area, and isolation on the macroinvertebrate fauna of rapids in North Swedish Rivers. *Regulated Rivers: Research and Managment* **12**, 433-445.

Equihua, M. 1990 Fuzzy clustering of ecological data. *Journal of Ecology*. **78** 519-534.

Evans, L. J. & Norris, R. H. 1997 Prediction of benthic macroinvertebrate composition using microhabitat characteristics derived from stereo photography. *Freshwater Biology* **37**, 621-633.

Eyre, M. D., Carr, R., McBlane, R. P. & Foster, G. N. 1992 The effects of varying site-water duration on the distribution of water beetle assemblages, adults and larvae (Coleoptera, Haliplidae, Dytiscidae, Hydrophilidae). *Archiv Fur Hydrobiologie* **124**, 281-291.

Eyre, M. D., Foster, G. N. & Young, A. G. 1993 Relationships between water-beetle distributions and climatic variables - a possible index for monitoring global climatic-change. *Archiv Fur Hydrobiologie* **127**, 437-450.

Fitter, R. & Manuel, R. 1994 *Lakes, Rivers and Streams of Britain and North-West Europe*. Collins Photo Guide. Hong Kong: Harper Collins Publishers.

Fjellheim, A. 1996 Distribution of benthic invertebrates in relation to stream flow characteristics in a Norwegian river. *Regulated Rivers-Research & Management* **12**, 263-271.

Fjellheim, A., Havardstun, J., Raddum, G. G. & Schnell, O. A. 1993 Effects of increased discharge on benthic invertebrates in a regulated river. *Regulated Rivers-Research & Management* **8**, 179-187.

Fox, A. M. & Murphy, K. J. 1990a The efficacy and ecological impacts of herbicide and cutting regimes on the submerged plant-communities of 4 british rivers .1. A comparison of management efficacies. *Journal of Applied Ecology* **27**, 520-540.

Fox, A. M. & Murphy, K. J. 1990b The efficacy and ecological impacts of herbicide and cutting regimes on the submerged plant-communities of 4 british rivers .2. A multivariate-analysis of the effects of management regimes On macrophyte communities. *Journal of Applied Ecology* **27**, 541-548.

Fozzard, I.R., Doughty, C.R. & Clelland, B.E. 1994 Invertebrates. *The Freshwaters of Scotland - A National Resource of International Significance*. (Ed. Maitland, P.S., Boon, P. J. & McLusky, D.S.) John Wiley & Sons. Chichester.

Gauch, H. G. 1982 *Multivariate Analysis in Community Ecology*. Cambridge: Cambridge University Press.

Georgian, T. & Thorp, J. H. 1992 Effects of microhabitat selection on feeding rates of net-spinning caddisfly Larvae. *Ecology* **73**, 229-240.

Giller, P. S. & Malmquist, B. 1998 *The Biology of Streams and Rivers*. Biology of habitats. Oxford: Oxford University Press.

Gilvear, D. & Bradley, S. 1997 Geomorphological adjustment of a newly engineered upland sinuous gravel-bed river diversion: Evan Water, Scotland. *Regulated Rivers: Research and Management* **13**, 377-389.

Golubkov, S. M., Tiunova, T. M. & Kocharina, S. L. 1992 Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. *Aquatic Insects* **14**, 137-144.

Gore, J. A., Crawford, D. J. & Addison, D. S. 1998 An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *Regulated Rivers-Research & Management* **14**, 69-77.

Gray, J. S. 1987 Species-abundance patterns. In *Organisation of Communities; Past and Present* (ed. J. H. R. Gee & P. S. Giller), pp. 53-68. Oxford: Blackwell Scientific Publications.

Gregg, W. W. & Rose , F. L. 1982 The effects of aquatic macrophytes on the stream microenvironment. *Aquatic Botany* **14**, 309-324.

Guinand, B., Tachet, H. & Roux, C. 1994 Longitudinal distribution and ecophysiological charcteristics of *Hydropsyche exocellata* (Trichoptera: Hydropsychidae) in large rivers. *Ecography* **17**, 189-197.

Gurtz, M. E. & Wallace, J. B. 1984 Substrate-mediated response of stream invertebrates to disturbance. *Ecology* **65**, 1556-1569.

Hammond, C. & Merrit, R. 1983 *The Dragonflies of Great Britain and Ireland*. Colchester: Harley Books, Martins, Great Horkesley, Essex CO6 4AH.

Hansen, R. A., Hart, D. D. & Merz, R. A. 1991 Flow mediates predator-prey interactions between triclad flatworms and larval black flies. *Oikos* **60**, 187-196.

Hanski, I. 1994 Metapopulation Ecology. In *Spatial and Temporal Aspects of Population Processes* (ed. O. E. Rhodes Jr). Georgia: University of Georgia.

Harper, D., Ebrahimnezhad, M. & Cot, F. C. I. 1998 Artificial riffles in river rehabilitation: setting the goals and measuring the successes. *Aquatic Conservation-Marine and Freshwater Ecosystems* **8**, 5-16.

Harrison, S. S. C. & Hildrew, A. G. 1998 Distribution dynamics of epilithic insects in a lake littoral. *Archiv Fur Hydrobiologie* **143**, 275-293.

Hart, D. D. 1991 Feeding postures of suspension-feeding larval black flies - The conflicting demands of drag and food acquisition. *Oecologia* **85**, 457-463.

Hart, D. D. 1992 Community organization in streams - the importance of species interactions, physical factors, and chance. *Oecologia* **91**, 220-228.

Hart, D. D., Clark, B. D. & Jasentuliyana, A. 1996 Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography* **41**, 297-308.

Hart, D. D. & Latta, S. C. 1986 Determinants of ingestion rates in filter-feeding larval blackflies (Diptera, Simuliidae). *Freshwater Biology* **16**, 1-14.

Hawkins, C. P., Hogue, J. N., Decker, L. M. & Feminella, J. W. 1997 Channel morphology, water temperature, and assemblage structure of stream insects. *Journal of the North American Benthological Society* **16**, 728-749.

Hearne, J., Johnson, I. & Armitage, P. 1994 Determination of ecologically acceptable flows in rivers with seasonal-changes in the density of macrophyte. *Regulated Rivers-Research & Management* **9**, 177-184.

Hey, R. D., Heritage, G. L. & Patterson, M. 1994 Impact of flood alleviation schemes on aquatic macrophytes. *Regulated Rivers: Research and Managment* **9**, 103-119.

Hickin, N. E. 1967 *Caddis Larvae of the British Trichoptera.* London: Hutchinson & Co. Ltd.

Hildrew, A. G. & Giller, P. S. 1994 Patchiness, species interactions and disturbance in the stream benthos. In *Aquatic Ecology, Scale, Pattern and Process* (ed. P. S. Giller, A. G. Hildrew & D. G. Raffaelli), pp. 649. Oxford: Blackwell Scientific Ltd.

Hoey, T. B., Smart, D. W. J., Pender, G. & Metcalfe, N. 1998 *Engineering Methods for Scottish Gravel Bed Rivers.* SNH Review No. 47. Battleby: Scottish Natural Heritage.

Holomuzki, J. R. 1996 Effects of substrate and predator type on microdistributions and drift of a lotic mayfly. *Journal of the North American Benthological Society* **15**, 520-528.

Hughes, J. M., Bunn, S. E., Hurwood, D. A. & Cleary, C. 1998 Dispersal and recruitment of *Tasiagma ciliata* (Trichoptera: Tasimiidae) in rainforest streams, south-eastern Australia. *Freshwater Biology* **39**, 117-127.

Hughes, J. M., Mather, P. B., Sheldon, A. L. & Allendorf, F. W. 1999 Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biology* **41**, 63-72.

Huhta, A., Muotka, T. & Tikkanen, P. 1995 Diel foraging periodicity of lotic mayfly (Ephemeroptera) nymphs during the sub-arctic summer. *Archiv Fur Hydrobiologie* **134**, 281-294.

Hurlbert, S. H. 1984 Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187-211.

Huryn, A. D. & Wallace, J. B. 1988 Community structure of Trichoptera in a mountain stream - spatial patterns of production and functional-organization. *Freshwater Biology* **20**, 141-155.

Hutchinson, G. E. 1957 *Geography, physics and chemistry. A Treatise on Limnology.* New York: John Wiley & Sons, inc.

Hynes, H. B. N. 1972 *The Ecology of Running Waters.* Liverpool: Liverpool University Press.

Hynes, H. B. N. 1976 Biology of Plecoptera. *Annual Rview of Entomology* **21**, 135-153.

Hynes, H. B. N., Williams, D. D. & Williams, N. E. 1976 Distribution of the benthos within the substratum of a Welsh mountain stream. *Oikos* **27**, 307-310.

Jenkins, R. A., Wade, K. R. & Pugh, E. 1984 Macroinvertebrate habitat relationships in the Tefi catchment and significance to conservation. *Freshwater Biology* **14**, 23-42.

Jeppesen, E., Iversen, T. M., Sand-Jensen, K. & Jorgensen, C. P. 1984 Økologiske konsekvenser af reduceret vandføring i Susån. In *Biologiske processor og vandvalitets-forhold.*, vol. 2. Copenhagen: Miljøstryrelsen.

Johnson, I. W., Elliott, C. R. N. & Gustard, A. 1995 Using the IFIM to model salmonid fish habitat in the River Allen, England. *Bulletin Francais De La Peche Et De La Pisciculture* , 355-363.

Johnson, I. W. & Law, F. M. 1995 Computer-models for quantifying the hydro-ecology of British rivers. *Journal of the Chartered Institution of Water and Environmental Management* **9**, 290-297.

Jones, N. V., Litterick, M. R. & Pearson, R. G. 1977 Stream flow and the behaviour of caddis larvae. In *Proceedings of the Second International Conference on Trichoptera.* Junk, The Hague.

Jongman, R. H. G., Ter Braak, C. J. F. & Van Tongeren, O. F. R. 1988 *Data Analysis in Community and Landscape Ecology.* Cambridge: Cambridge University Press.

Jowett, I. G. 1993 A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research* **27**, 241-248.

Jowett, I. G. 1998 Hydraulic geometry of New Zealand rivers and its use as a preliminary method of habitat assessment. *Regulated Rivers-Research & Management* **14**, 451-466.

Jowett, I. G. & Richardson, J. 1995 Habitat preferences of common riverine New Zealand native fishes and implications for flow managment. *New Zealand Journal of Marine and Freshwater Research* **29**, 13-23.

Jowett, I. G., Richardson, J., Biggs, B. J. F., Hickey, C. W. & Quinn, J. M. 1991 Microhabitat preferences of benthic invertebrates and the development of generalized *Deleatidium* spp habitat suitability curves, applied to 4 New-Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **25**, 187-199.

Jowett, I. G. 1997 Instream flow methods: A comparison of approaches. *Regulated Rivers-Research & Management* **13**, 115-127.

Keckeis, H. & Schiemer, F. 1992 Food-consumption and growth of larvae and juveniles of 3 cyprinid species at different food levels. *Environmental Biology of Fishes* **33**, 33-45.

Kiel, E. & Frutiger, A. 1997 Behavioural responses of different blackfly species to short -term oxygen depletion. *International Revue der gesampten Hydrobiologie* **82**, 107-120.

Koetsier, P. & Bryan, C. F. 1995 Effects of abiotic factors on macroinvertebrate drift in the lower Mississippi river, Louisiana. *American Midland Naturalist* **134**, 63-74.

Kohler, S. L. 1985 Identification of stream drift mechanisms: An experimental and observational approach. *Ecology* **66**, 1749-1761.

Kratz, K. W. 1996 Effects of stoneflies on local prey populations - mechanisms of impact across prey density. *Ecology* 77, 1573-1585.

Lacoursiere, J. O. 1991 A laboratory study of fluid flow and microhabitat selection by larvae of *Simulium vittatum* (Diptera: Simuliidae). *Canadian Journal of Zoology* **70**, 582-596.

Lamouroux, N. 1993 Comment on 'The nature of the fluid boundary layer and the selection of parameters for benthic ecology' (Carling, 1992). *Freshwater Biology* **30**, 331-332.

Lancaster, J. 1992 Diel variations in the effect of spates on mayflies (Ephemeroptera, *Baetis). Canadian Journal of Zoology* **70**, 1696-1700.

Lancaster, J. 1999 Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology* **41**, 605-619.

Lancaster, J. & Hildrew, A. G. 1993a Characterising in-stream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1663-1675.

Lancaster, J. & Hildrew, A. G. 1993b Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of the North American Benthological Society* **12**, 385-393.

Lancaster, J., Hildrew, A. G. & Townsend, C. R. 1990 Stream-flow and predation effects on the spatial dynamics of benthic invertebrates. *Hydrobiologia* **203**, 177-190.

Langan, S. J., Wade, A. J., Smart, R., Edwards, A. C., Soulsby, C., Billett, M. F., Jarvie, H. P., Cresser, M. S., Owen, R. & Ferrier, R. C. 1997 The prediction and management of water quality in a relatively unpolluted major Scottish catchment: Current issues and experimental approaches. *Science of the Total Environment* **194**, 419-435.

Layzer, J. B. & Madison, L. M. 1995 Microhabitat use by fresh-water mussels and recommendations for determining their instream flow needs. *Regulated Rivers-Research & Management* **10**, 329-345.

Leader, J. P. 1976 Marine caddis flies (Trichoptera: Philanisidae). In *Marine Insects* (ed. L. Cheng), pp. 581. Amsterdam: North-holland publishing company.

LeRoy Poff, N. 1996 A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* **36**, 71-91.

Levins, R. 1969 Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237-240.

Lynch, J. M. & Murray, D. A. 1994 Fishery rehabilitation enhancment following arterial drainage in Ireland. *Verh. Internat. Verein. Limnol.* **25**, 1502-1508.

Macan, T. T. 1963 *Freshwater Ecology*: Longmans, Green & Co. Ltd.

Macan, T. T. 1977 *A Key to the British Fresh- and Brackish-water Gastropods with Notes on their Ecology*. Scientific Publication No. 13. Far Sawrey, Ambleside, Cumbria: Freshwater Biological Association.

Maitland, P. S. 1977 *A Coded Checklist of Animals Occurring in Fresh Water in the British Isles*: Institute of Terrestrial Ecology.

Maitland, P. S. 1990 *Biology of Freshwaters*. Tertiary Level Biology. Glasgow & London: Blackie.

Makipaa, R. 1999 Response patterns of *Vaccinium myrtillus* and V-*vitis-idaea* along nutrient gradients in boreal forest. *Journal of Vegetation Science* **10**, 17-26.

Malicky, H. 1981 The phenology of dispersal of several caddisfly (Trichoptera) species in the island of Crete. In *Third International Symposium on Trichoptera.* (ed. G.P. Moretti). Junk The Hague, 157-163.

Malmquist, B. & Otto, C. 1987 The influence of substrate stability on the compositon of stream benthos: an experimental study. *Oikos* **48**, 33-38.

Marshall, E. J. P. & Westlake, D. F. 1990 Water velocities around water plants in chalk streams. *Folia geobotanic et phytotaxonomica* **25**, 279-289.

Matthaei, C. D., Uehlinger, U. & Frutiger, A. 1997 Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology* **37**, 61-77.

Matthaei, C. D., Uehlinger, U., Meyer, E. I. & Frutiger, A. 1996 Recolonization by benthic invertebrates after experimental disturbance in a swiss prealpine river. *Freshwater Biology* **35**, 233-248.

McCracken, D.I. 1994 A fuzzy classification of moorland ground beetle (Coleoptera: Carabidae) and plant communities. *Pedobiologia* **38** 12-27.

McCune, B. 1997 Influence of noisy environmental data on canonical analysis. *Ecology* **78**, 2617-2623.

McKirdy, A. 1999 *A Landscape Fashioned by Geology: Scotland - Creation of its Natural landscape*: Scottish Natural Heritage.

McShaffrey, D. & McCafferty, W. P. 1987 The behaviour and form of *Psephenus herricki*(DeKay) (Coleoptera: Psephenidae) in realtion to water flow. *Freshwater Biology* **18**, 319-324.

Merrit, R. W. & Cummins, K. W. 1979 *An Introduction to Aquatic Insects*. Dubuque, Iowa: Kendall/Hunt Publishing.

Milhous, R. T., Wegner, D. L. & Waddle, T. 1984 User's guide to the physical habitat simulation system. *US Fish and Wildlife Service Biological Services Program* **FWS/OBS-81/43**.

Miller, P. 1987 *Dragonflies*. Naturalists' handbooks 7. Cambridge: Cambridge University Press.

Minshall, G. W. 1984 Aquatic insect -substratum relationships. In *Ecology of Aquatic Insects*.

Minshall, G. W., Cummins, K. W., Petersen, R. C., Cushing, C. E., Bruns, D. A., Sedell, J. R. & Vannote, R. L. 1985 Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1045-1055.

Moog, D.B. & Jirka, G.H. 1999 Stream reaeration in nonuniform flow: Macroroughness enhancement. Journal of Hydraulic Engineering-ASCE, Vol.125, No.1, pp.11-16

Morgan, N. C. & Egglishaw, H. J. 1966 A survey of the bottom fauna of streams in the Scottish Highlands. Pt. I. Composition of the fauna. *Hydrobiologia* **25**, 181-211.

Moss, B. 1988 *Ecology of Freshwaters Man and Medium*. Oxford: Blackwell Scientific Publications.

Nagell, B. & Larshammar, P. 1981 Critical oxygen-demand in Plecoptera and Ephemeroptera nymphs as determined by 2 methods. *Oikos* **36**, 75-82.

Newbury, R. & Gaboury, M. 1993 Exploration and rehabilitation of hydraulic habitats in streams using principles of fluvial behaviour. *Freshwater Biology* **29**, 195-210.

Nowell, A. R. M. & Church, M. 1979 Turbulent flow in a depth-limited boundary layer. *Journal of Geophysical Research* **84**, 4816-4823.

O'Connor, N. A. 1991 The effects of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland stream. *Oecologia* , 504-512.

Ormerod, S. J. 1988 The micro-distribution of aquatic macroinvertebrates in the Wye river system: the result of biotic or abiotic factors? *Freshwater Biology* **20**, 241-247.

Otto, C. 1976 Factors affecting the drift of *Potamophylax cingulatus* (Trichoptera) larvae. *Oikos* **27**, 93-100.

Palmer, C., O Keeffe, J. & Palmer, A. 1993a Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, Eastern Cape, South-Africa .2. Functional-morphology and behaviour. *Freshwater Biology* **29**, 455-462.

Palmer, C., O Keeffe, J., Palmer, A., Dunne, T. & Radloff, S. 1993b Macroinvertebrate functional feeding groups in the middle and lower reaches of the buffalo river, Eastern Cape, South-Africa .1. dietary variability. *Freshwater Biology* **29**, 441-453.

Peeters, E. & Gardeniers, J. J. P. 1998 Logistic regression as a tool for defining habitat requirements of two common gammarids. *Freshwater Biology* **39**, 605-615.

Petts, G., Maddock, I., Bickerton, M. & Ferguson, A. J. D. 1995 Linking Hydrology and Ecology: The scientific basis of river managment. In *The Ecological Basis of River Management* (ed. D. M. Harper & A. J. D. Ferguson), pp. 1-16. Chichester: John Wiley & Sons.

Petts, G. E. & Bickerton, M. A. 1994 Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology* **32**, 375-386.

Poff, N. L., Palmer, M. A., Angermeier, P. L., Vadas, R. L., Hakenkamp, C. C., Bely, A., Arensburger, P. & Martin, A. P. 1993 Size structure of the metazoan community in a piedmont stream. *Oecologia* **95**, 202-209.

Poff, N. L. & Ward, J. V. 1991 Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1926-1936.

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., Welcomme, R. L. & Winterbourn, M. J. 1988 Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* **7**, 503-524.

Puckridge, J. T., Sheldon, F., Walker, K. F. & Boulton, A. J. 1998 Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**, 55-72.

Quinn, J. M. & Hickey, C. W. 1994 Hydraulic parameters and benthic invertebrate distributions in 2 gravel-bed New-Zealand rivers. *Freshwater Biology* **32**, 489-500.

Quinn, J. M., Hickey, C. W. & Linklater, W. 1996 Hydraulic influences on periphyton and benthic macroinvertebrates - simulating the effects of upstream bed roughness. *Freshwater Biology* **35**, 301-309.

Raddum, G. G. & Fjellheim, A. 1993 Life-cycle and production of *Baetis rhodani* in a regulated river in western Norway - comparison - of pre-regulation and post-regulation conditions. *Regulated Rivers-Research & Management* **8**, 49-61.

Reynolds, C. S. 1998 The state of freshwater ecology. *Freshwater Biology* **39**, 741-753.

Rincon, P. A. & LobonCervia, J. 1997 Temporal patterns in macroinvertebrate drift in a northern Spanish stream. *Marine and Freshwater Research* **48**, 455-464.

Rosillon, D. 1988 Food preference and relative influence of temperature and food quality on life-history characteristics of a grazing mayfly, *Ephemerella-ignita* (poda). *Canadian Journal of Zoology* **66**, 1474-1481.

Rossaro, B. & Pietrangelo, A. 1993 Macroinvertebrate distribution in streams: a comparision of CA ordination with biotic indices. *Hydrobiologia* **263**, 109-118.

Rutt, G. P., Weatherley, N. S. & Ormerod, S. J. 1989 Microhabitat availibility in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. *Freshwater Biology* **22**, 247-261.

Sabbatini, M. R. & Murphy, K. J. 1996 Response of *Callitriche* and *Potamogeton* to cutting, dredging and shade in English drainage channels. *Journal of Aquatic Plant Management* **34**, 8-12.

Saetersdal, M. & Birks, H. J. B. 1997 A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *Journal of Biogeography* **24**, 127-152.

Sand-Jensen, K. 1998 Influence of submerged macrophytes on sediment composition and near- bed flow in lowland streams. *Freshwater Biology* **39**, 663-679.

Sand-Jensen, K. & Madsen, T. V. 1992 Patch dynamics of the stream macrophyte, *Callitriche-cophocarpa*. *Freshwater Biology* **27**, 277-282.

Sand-Jensen, K. & Mebus, J. R. 1996 Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos* **76**, 169-180.

Scarsbrook, M. R. & Townsend, C. R. 1993 Stream community structure in relation to spatial and temporal variation: a habitat template study of two contrasting New Zealand streams. *Freshwater Biology* **29**, 395-410.

Schiemer, F. & Wieser, W. 1992 Food and feeding, ecomorphology, energy assimilation and conversion in cyprinids - epilogue. *Environmental Biology of Fishes* **33**, 223-227.

Schmidt - Nielson, K. 1990 *Animal Physiology. Adaptation and Environment.* Cambridge: Cambridge University Press.

Sidney, S. 1956 *Nonparametric Statistics for the Behavioural Sciences.* Tokyo: McGraw-Hill Book Company, Inc.

Smith, I. R. 1975 *Turbulence in Lakes and Rivers.* Scientific publication no. 29. Ambleside: Freshwater Biological Association.

Smith, I. R. & Lyle, A. A. 1994 Running Waters. In *The Freshwaters of Scotland, A National Resource of International Significance* (ed. P. S. Maitland, P. J. Boon & D. S. Mclusky), pp. 17-34: John Wiley & Sons.

Smith, J. A. & Dartnall, A. J. 1980 Boundary layer control by water pennies (Coleoptera: Psephenidae). *Aquatic Insects* **2**, 65-72.

Southwood, T. R. E. 1977 Habitat: the template for ecological strategies? *Journal of Animal Ecology* **46**, 337-365.

Southwood, T. R. E. 1988 Tactics, strategies and templates. *Oikos* **52**, 3-18.

Statzner, B. 1988 Growth and Reynolds-number of lotic macroinvertebrates - a problem for adaptation of shape to drag. *Oikos* **51**, 84-87.

Statzner, B. & Higler, B. 1985 Questions and comments on the river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1038-1044.

Statzner, B. & Higler, B. 1986 Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* **16**, 127-139.

Statzner, B. & Holm, T. F. 1982 Morphological adaptations of benthic invertebrates to stream-flow - an old question studied by means of a new technique (laser doppler anemometry). *Oecologia* **53**, 290-292.

Statzner, B. & Holm, T. F. 1989 Morphological adaptation of shape to flow: Microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. *Oecologia* **78**, 145-157.

Strevens, A. P. 1999 Impacts of groundwater abstraction on the trout fishery of the River Piddle, Dorset; and an approach to their alleviation. *Hydrological Processes* **13**, 487-496.

Surber, E. W. 1937 Rainbow trout and bottom fauna in one mile of stream. *Transactions of American Fisheries Society* **66**, 193-202.

Survey, G. 1971 Geological map of Great Britain: Sheet 1. Chessington: Ordance Survey.

Survey, G. 1977 Geological Survey, North Sheet: Institute of Geological Sciences.

Svensson, B. W. 1972 Flight periods, ovarian maturation and mating in Trichoptera at a South Swedish stream. *Oikos* **23**, 370-383.

Swales, S. & O'Hara, K. 1980 Instream habitat improvement devices and their use in freshwater fisheries management. *Journal of Environmental Management* **10**, 167-179.

ter Braak, C. J. F. & Prentice, I. C. 1988 A theory of gradient analysis. *Advances in Ecological Research* **18**. 271-317.

ter Braak 1997, 1998 *Canoco for Windows*. Wageningen.

ter Braak, C. J. F. & Smilauer, P. 1998 *CANOCO Reference Manual and User's Guide to Canoco for Windows*. Ithaca: Microcomputer Power.

Thorup, J. 1966 Substrate type and its value as a basis for the delimitation of bottom fauna communities in running waters. *Special publication number4 Pymatuning Labortory of Ecology University of Pittsburg* , 59-74.

Tikkanen, P., Muotka, T. & Huhta, A. 1994 Predator detection and avoidance by lotic mayfly nymphs of different size. *Oecologia* **99**, 252-259.

Tockner, K. & Schiemer, F. 1997 Ecological aspects of the restoration strategy for a river-floodplain system on the Danube River in Austria. *Global Ecology and Biogeography Letters* **6**, 321-329.

Tokeshi, M. 1993 On the evolution of commensalism in the Chironomidae. *Freshwater Biology* **29**, 481-489.

Tokeshi, M. 1994 Community ecology and patchy freshwater habitats. In *Aquatic Ecology: Scale, Pattern and Process* (ed. P. S. Giller, A. G. Hildrew & D. G. Raffaelli), pp. 63-92. Oxford: Blackwell Science.

Townsend, C. R. 1980 *The Ecology of Streams and Rivers*. Studies in Biology no. 122. Southhampton: Camelot Press Ltd.

Townsend, C. R. 1989 The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**, 36-50.

van't Woudt, B. D. & Nicolle, K. 1978 Flow processes below a gravelly riverbed. *Journal of Hydrology (N.Z.)* **17**, 103-120.

Vogel, S. 1994 *Life in Moving Fluids The Physical Biology of Flow*. Princeton, New Jersey: Princeton University Press.

Walker, P. M. B. 1995 *Dictionary of Science and Technology*. Edinburgh & New York: Larousse.

Wallace, I. D. 1981 A key to larvae of the family Leptoceridae (Trichoptera) in Great- Britain and Ireland. *Freshwater Biology* **11**, 273-297.

Wallace, I. D., Wallace, B. & Philipson, G. N. 1990 *A Key to the Case Bearing Caddis Larvae of Britain and Ireland*. Scientific Publication No. 53. Far Sawrey: Freshwater Biological Association.

Walton Jr, O. E. 1978 Substrate attachment by drifting aquatic insect larvae. *Ecology* **59**, 1023-1030.

Ward, J. V., Bretschko, G., Brunke, M., Danielopol, D., Gibert, J., Gonser, T. & Hildrew, A. G. 1998 The boundaries of river systems: the metazoan perspective. *Freshwater Biology* **40**, 531-569.

Waringer, J. A. 1987 Spatial-distribution of Trichoptera larvae in the sediments of an Austrian mountain brook. *Freshwater Biology* **18**, 469-482.

Waringer, J. A. 1989a Life cycle, horizontel microdistribution and current resistance of *Allogamus auricollis* (Trichoptera: Limnophilidae) in an Austrian mountain brook. *Freshwater Biology* **22**, 177-188.

Waringer, J. A. 1989b Resistance of a cased caddis larva to accidental entry into the drift - the contribution of active and passive elements. *Freshwater Biology* **21**, 411-420.

Waringer, J. A. 1993 The drag coefficient of cased caddis larvae from running waters - experimental-determination and ecological applications. *Freshwater Biology* **29**, 419-427.

Webb, B. W. & Walling, D. E. 1993 Temporal variability in the impact of river regulation on thermal regime and some biological implications. *Freshwater Biology* **29**, 167-182.

Weissenberger, J., Spatz, H., Emanns, A. & Schwoerbel, J. 1991 Measurement of lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m/s. *Freshwater Biology* **25**, 21-31.

Welcomme, R. L. 1992 River conservation - Future perspectives. In *River Conservation and Management* (ed. P. J. Boon, P. Calow & G. E. Petts), pp. 453-462. Chichester: John Wiley & Sons.

Wells, A. 1992 The 1st parasitic Trichoptera. *Ecological Entomology* **17**, 299-302.

Werritty, A., Brazier, V., Gordon, J. E. & McManus, J. 1994 Geomorphology. In *The Freshwaters of Scotland, A National Resource of International Significance* (ed. P. S. Maitland, P. J. Boon & D. S. Mclusky), pp. 65-88: John Wiley & Sons.

Whetmore, S. H., Mackay, R. J. & Newbury, R. W. 1990 Characterization of the hydraulic habitat of *Brachycentrus - occidentalis*, a filter-feeding caddisfly. *Journal of the North American Benthological Society* **9**, 157-169.

Williams, D. D. & Feltmate, B. W. 1994 *Aquatic Insects*. Wallingford: CAB International.

Williams, D. D. & Smith, M. R. 1996 Colonisation dynamics of river benthos in response to local changes in bed charcterstics. *Freshwater Biology* **36**, 237-248.

Williams, D. D., Tavares, A. F. & Bryant, E. 1987 Respiratory device or camouflage - a case for the caddisfly. *Oikos* **50**, 42-52.

Wohl, D. L., Wallace, J. B. & Meyer, J. L. 1995 Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage-basin in the southern Appalachians (USA). *Freshwater Biology* **34**, 447-464.

Wohl, E. E., Vincent, K. R. & Merritts, D. J. 1993 Pool and Riffle Characteristics in Relation to Channel Gradient. *Geomorphology* **6**, 99-110.

Wright, J. F. 1992 Spatial and temporal occurrence of invertebrates in a chalk stream,. *Hydrobiologia* **248**, 11-30.

Wright, J. F., Blackburn, J. H., Westlake, D. F., Furse, M. T. & Armitage, P. D. 1995 Anticipating the consequences of river management for the conservation of macroinvertebrates. In *The Ecological Basis of River Management* (ed. D. M. Harper & A. J. D. Ferguson), pp. 137-150. Chichester: John Wiley & Sons.

Young, W. J. 1992 Clarification of the criteria used to identify near-bed flow regimes. *Freshwater Biology* **28**, 383-391.

Young, W. J. 1993 Field techniques for the classification of near-bed flow regimes. *Freshwater Biology* **29**, 377-383.

Appendix I: Definitions of flow units and parameters

Symbol	Definition
D	Water depth (m)
Fr	Froude number
g	Acceleration due to gravity 9.8m^2s^{-1}
k_s	Nikuradse's roughness
Re	Reynolds number
Re_*	Reynolds roughness number
U	Water velocity measured at 0.4D from the substrate. It equates to depth averaged velocity in a full developed boundary layer.
u_*	Shear velocity (ms^{-1})
z_0	Characteristic Roughness length (m)
δ	Thickness of the laminar sublayer (mm)
ν	kinematic viscosity ($\cong 1 \times 10^{-6}$ m^2s^{-1} at 20 °C)
τ_o	Boundary shear stress (Nm^{-2})

Appendix II: Log plotting of velocity profiles

Introduction

Plots of velocity against natural log of depth, show a linear relationship from which a number of hydraulic variables can be estimated. Variables generated from this relationship and presented in this thesis were produced using a Microsoft Excel template file designed by Dr. Trevor Hoey of Glasgow University Department of Geography and Topographic Sciences. A large number of these files were generated during analysis, River Etive (49), Duneaton Water (52) and Blane Water (42), see appendix III. An example from one river is given showing the generation of derived variables from raw data. For all other regressions summaries of the variables generated are presented. Velocity profiles were chosen to be used in further analysis if their regression lines were statistically significant. I checked for patterns in the data that may bias further analysis.

Methods

When the velocity profile is plotted on a lognormal co-ordinate shear velocity (u*) and equivalent bed hydraulic roughness (k_s) can be calculated.

Shear velocity is inversely proportional to the gradient of the velocity profile and z_0 (characteristic roughness length) can be calculated by extrapolating the regression line to zero velocity. The variable z_0 can be taken as an estimate of k_s. These variables are useful in classifying near bed flow. Reynolds roughness number (Re_*) can be calculated from these two variables.

$$\mathrm{Re}_* = u_* k_s / v$$

Critical values of Re_* delineate flow as to the presence of the laminar sublayer of the boundary layer. Where the laminar sublayer is present its thickness (δ) can be estimated as follows:

$\delta = 11.6v / u_*$

Working Example: Sample point **Blane** Water Section **A**, **Transect 1**, Sample **A**. (BLAT1SA)

Table ii-1, Raw data from BLAT1SA showing natural log values for depth.

Height above bed (m)	ln (ht. Above bed)	Velocity (m/s)
0.01	-4.61	0.26
0.012	-4.42	0.28
0.014	-4.27	0.30
0.018	-4.02	0.21
0.02	-3.91	0.37
0.04	-3.22	0.41
0.06	-2.81	0.46
0.08	-2.53	0.49
0.1	-2.30	0.52
0.12	-2.12	0.51

The plot of log depth against velocity is visually checked for a linear relationship between the two variables, Figure ii-1. In this case the left most point is an obvious outlier and does not follow the line described by the other points but it is not removed from the analysis. The linear relationship between ln depth and velocity in fully developed boundary layers is a well described in the literature and is an accepted fact by both physicists, hydrologists and geomorphologists hence it is acceptable to remove rogue points at this stage that deviate from a clear pattern. It has been suggested that the estimation of bed shear stress from velocity profiles in a shallow river environment can be improved by using only the section of the profile from close to the bed (Biron *et al.* 1998).

In a number of cases (R.Etive 14, Duneaton Water 2, Blane Water 0) I did remove points which did not follow the log-linear relationship. This was exclusively where points high up in a profile failed to follow the log-linear relationship, Figure ii-2. In the example plotted in Figure ii-2 the removal of the top 4 points of the plot improved the fit from $R^2 = 0.31$ to $R^2 = 0.87$.

There are a number of situations were velocity profiles of this type are likely to happen, ' *...non-logarithmic layers may occur in strongly accelerating or de-accelerating flow such as occurs in river reaches which narrow or widen rapidly. The logarithmic profile may be distorted by spatial variation in the mixture of roughness types on the bed, or by extreme bed roughness such as occurs over dunes and over large rocks. ..... However even in these circumstances it is possible to obtain near log-normal distributions of velocity, from close to the bed, which can be used to estimate the local bed shear stress.*' from (Carling 1992). The second instance where bed roughness is the important factor would occur at the 3 rivers examined in this study.

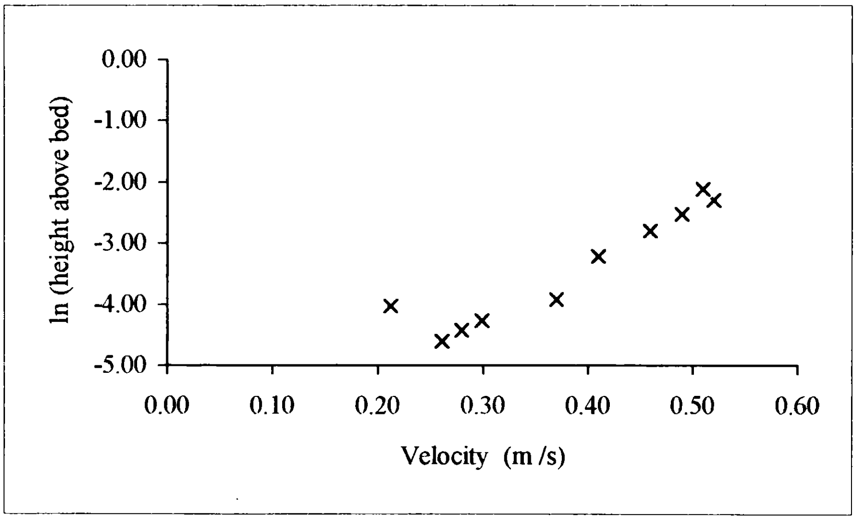

Figure ii-1 Velocity (u) measured at a number of depths above a single point on the stream bed plotted against ln depth (D).

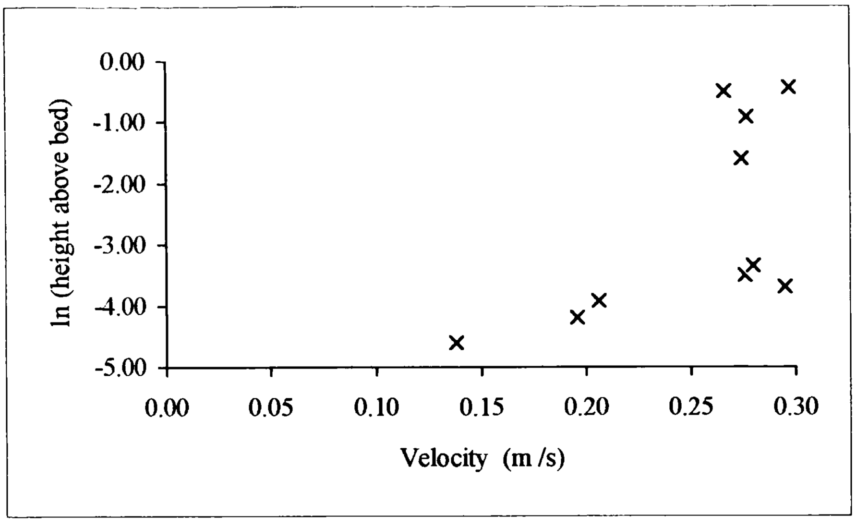

Figure ii-2 Plot from River Etive data, section A, Transect 4, sample c showing the breakdown of log linear relationship between depth and velocity higher up the water column.

Results

Estimates of the variables generated for our working example are given in table ii-2:

Table ii-2, Estimates of flow parameters from log normal plot of velocity against depth for River Etive sample A4C.

Variable	Estimate
r^2	0.87
Gradient	0.11
Intercept	0.77
z_0	0.001136
u*	0.0454
tau	2.06
s.e. grad	1.67E-02
s.e. tau	6.07E-01
Umax	0.53
U profile	0.42
U real	0.42
U at 0.37 depth	0.42
Fr	0.38

The R-squared value for each line was checked for its significance by looking up standard statistical tables. There was a clear relationship between the significance of profiles and mean water column velocity. The ranked plots showing the distribution of significant velocity profiles to mean water column velocity show the majority of non-significant profiles occurred in slow water in the Blane water and the Duneaton water Figures ii-3-5. This pattern was also evident in the River Etive but here there was also a strong scatter of non-significant profiles over the entire range of velocities sampled.

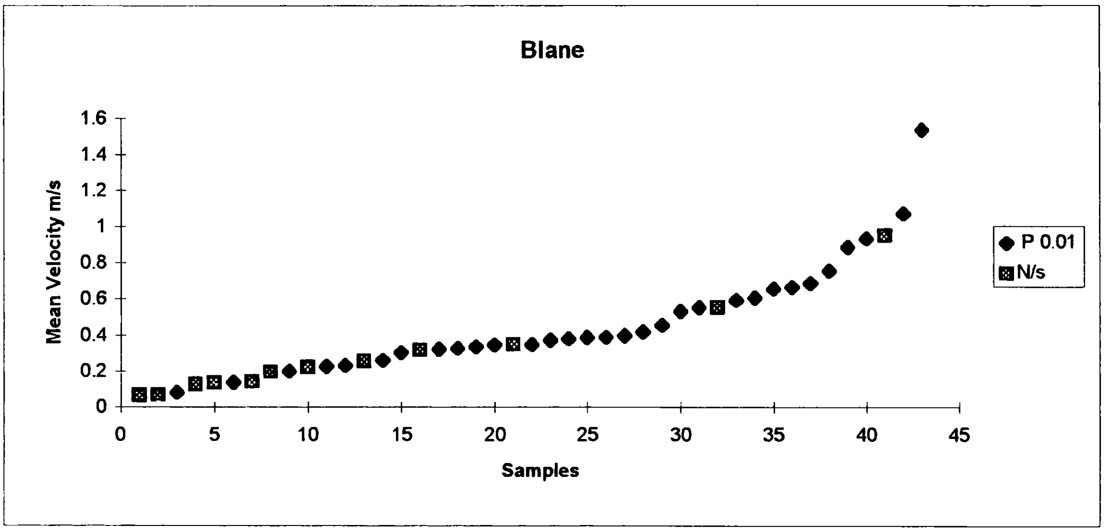

Figure ii-3 Rank order of Blane Water samples (velocity profiles) by increasing velocity mean water column velocity. Diamonds = statistically significant velocity profiles, squares = non significant velocity profiles.

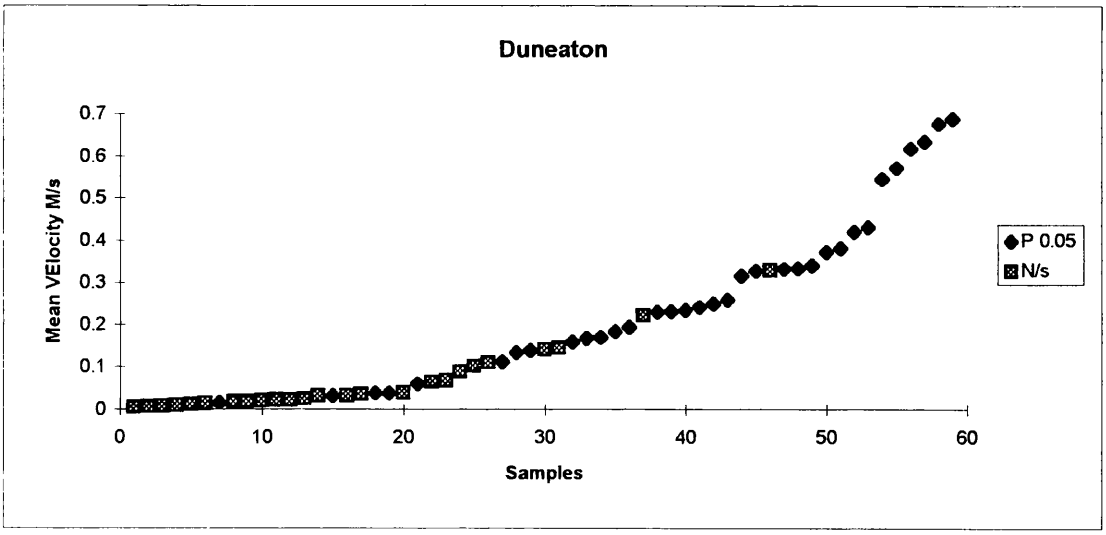

Figure ii-4 Rank order of Duneaton Water samples (velocity profiles) by increasing velocity mean water column velocity. Diamonds = statistically significant velocity profiles, squares = non significant velocity profiles.

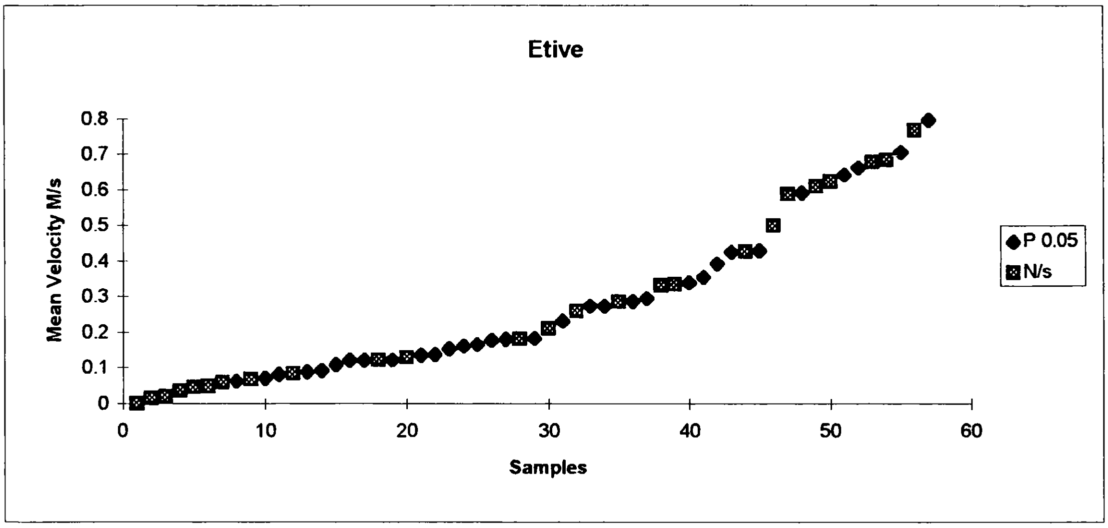

Figure ii-5 Rank order of River Etive samples (velocity profiles) by increasing velocity mean water column velocity. Diamonds = statistically significant velocity profiles, squares = non significant velocity profiles.

Discussion

The method worked well. The observed bias of non significant velocity profiles occurring in low velocity areas agrees with field observations. The most difficult velocity profiles to measure were in the slow shallows but also in the deeper water when slow. This often occurred behind large substrate elements where one would expect low flows. In the R. Etive large boulders frequently acted as weirs causing areas of both decelerating and accelerating water. The data presented here in combination with substrate measures can be used to identify the qualitative flow categories of skimming, wake interference and isolated roughness flows, but this aspect was not carried out (Davis & Barmuta 1989; Nowell & Church 1979).

Appendix III: Velocity profiles, raw data and regression analysis

Introduction

This appendix contains the velocity profiles for all sampling points where it was feasible to take a profile. Each site has its own table. The raw data is presented with the statistics for regression analysis of log depth (height above bed) against velocity. P values are either; n/s = not significant, * = P < 0.01, ** = P < 0.001, *** = P < 0.0001 and 5, where P <= 0.05.

Table III – 1, Blane Water data. Depth (m) are heights above the bed. Velocity (ms^{-1}) are 50 second averages. Sample codes are first two letters = site, third letter is section a or b, the number refers to the transect and the last two letters designate the sample along the transect. Six (14%) out of forty two velocity profiles were non-significant. Six invertebrate samples did not have velocity profiles taken with them at this site, this usually occurred where water velocity was not detectable, i.e. in the shallows.

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
blat1sa	9	0.87	***	60.00	Depth	0.010	0.012	0.014	0.018	0.020	0.040	0.060	0.080	0.100	0.120
					Velocity	0.261	0.280	0.299	0.212	0.370	0.410	0.460	0.490	0.520	0.510
blat1sb	10	0.97	***	256.80	Depth	0.010	0.012	0.014	0.018	0.020	0.060	0.090	0.120	0.150	0.170
					Velocity	0.014	0.036	0.013	0.047	0.088	0.370	0.520	0.580	0.580	0.540
blat1sc	8	0.98	***	325.00	Depth	0.012	0.014	0.018	0.070	0.120	0.170	0.220	0.250		
					Velocity	0.106	0.142	0.168	0.400	0.550	0.710	0.740	0.760		
blat2sa	10	0.96	***	244.00	Depth	0.010	0.012	0.014	0.018	0.020	0.060	0.100	0.140	0.180	0.200
					Velocity	0.134	0.183	0.235	0.249	0.284	0.400	0.450	0.570	0.590	0.530

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
blat3sa	10	0.95	***	175.00	Depth	0.010	0.012	0.014	0.018	0.020	0.060	0.100	0.140	0.180	0.190
					Velocity	0.108	0.193	0.217	0.255	0.231	0.320	0.390	0.470	0.520	0.490
blat3sb	10	0.98	***	449.00	Depth	0.010	0.012	0.014	0.018	0.020	0.100	0.170	0.250	0.300	0.320
					Velocity	0.148	0.235	0.233	0.273	0.322	0.470	0.610	0.690	0.700	0.680
blat3sc	10	0.97	***	364.00	Depth	0.010	0.012	0.014	0.018	0.020	0.090	0.160	0.230	0.280	0.290
					Velocity	0.182	0.309	0.298	0.350	0.310	0.570	0.660	0.760	0.766	0.720
blat4sa	10	0.96	***	208.00	Depth	0.010	0.011	0.012	0.013	0.014	0.015	0.020	0.050	0.100	0.130
					Velocity	0.148	0.131	0.138	0.138	0.175	0.176	0.184	0.249	0.291	0.350
blat4sb	10	0.16	n/s	2.66	Depth	0.010	0.012	0.014	0.018	0.020	0.022	0.040	0.050	0.060	0.070
					Velocity	0.103	0.191	0.139	0.250	0.152	0.105	0.119	0.142	0.233	0.360
blat5sa	10	0.82	***	42.64	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.090
					Velocity	0.060	0.061	0.078	0.065	0.074	0.076	0.082	0.089	0.098	0.089
blat5sb	10	0.96	***	209.80	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.120	0.180	0.230
					Velocity	0.101	0.132	0.168	0.169	0.198	0.193	0.278	0.360	0.420	0.370
blat5sc	10	0.97	***	362.00	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.160
					Velocity	0.192	0.184	0.223	0.217	0.211	0.236	0.299	0.420	0.460	0.480
blat6sa	10	0.66	*	18.59	Depth	0.010	0.012	0.014	0.018	0.020	0.040	0.080	0.100	0.120	0.150
					Velocity	0.280	0.272	0.271	0.288	0.287	0.289	0.340	0.360	0.460	0.360
blat6sb	10	0.96	***	220.00	Depth	0.010	0.012	0.014	0.018	0.020	0.060	0.100	0.140	0.180	0.210
					Velocity	0.132	0.144	0.162	0.165	0.149	0.286	0.350	0.400	0.430	0.380
blat6sc	9	0.96	***	182.00	Depth	0.010	0.012	0.014	0.018	0.020	0.050	0.100	0.150	0.200	

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.095	0.104	0.130	0.137	0.171	0.195	0.246	0.268	0.261	
blat7sa	9	0.89	***	62.57	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	
					Velocity	0.104	0.095	0.105	0.110	0.117	0.133	0.147	0.160	0.152	
blat7sb	10	0.91	***	95.32	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.080	0.110	0.140
					Velocity	0.166	0.145	0.153	0.174	0.179	0.186	0.201	0.273	0.310	0.310
blat7sc	10	0.91	***	97.89	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.070	0.120	0.160	0.210
					Velocity	0.204	0.212	0.202	0.225	0.166	0.257	0.304	0.390	0.420	0.430
blat8sa	10	0.77	***	31.70	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.080	0.120	0.150
					Velocity	0.151	0.153	0.185	0.182	0.211	0.208	0.209	0.216	0.238	0.266
blat8sb	10	0.97	***	303.90	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.070	0.120	0.170	0.230
					Velocity	0.118	0.120	0.159	0.157	0.198	0.145	0.270	0.330	0.360	0.380
blat8sc	10	0.75	**	27.90	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.090	0.170	0.250	0.330
					Velocity	0.101	0.086	0.139	0.134	0.100	0.113	0.134	0.170	0.253	0.275
blbt1sa	10	0.60	*	14.50	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.026	0.028	0.030
					Velocity	0.227	0.238	0.247	0.205	0.240	0.315	0.289	0.281	0.340	0.320
blbt1sb	10	0.63	*	16.40	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.120	0.170	0.180
					Velocity	0.390	0.380	0.410	0.470	0.520	0.560	0.540	0.630	0.630	0.540
blbt1sc	10	0.97	***	311.00	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.190
					Velocity	0.350	0.430	0.510	0.490	0.440	0.490	0.700	0.790	0.910	0.950
blbt2sa	10	-0.11	n/s	0.08	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.100
					Velocity	0.027	0.027	0.036	0.087	0.068	0.132	0.068	0.115	0.061	0.018

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
blbt2sb	10	0.27	n/s	4.30	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.028	0.030	0.032
					Velocity	0.115	0.119	0.145	0.160	0.193	0.220	0.181	0.189	0.210	0.135
blbt2sc	10	0.92	***	104.00	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.100	0.120
					Velocity	0.610	0.680	0.750	0.670	0.700	0.860	0.840	1.010	1.100	1.110
blbt3sa	10	0.86	***	56.40	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	0.060
					Velocity	0.252	0.310	0.263	0.282	0.300	0.370	0.470	0.410	0.550	0.640
blbt3sb	10	0.97	***	268.00	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.070	0.100	0.130
					Velocity	0.510	0.550	0.580	0.640	0.580	0.600	0.830	0.910	1.100	1.100
blbt3sc	10	0.70	*	22.40	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.100	0.130	0.160
					Velocity	0.370	0.600	0.760	0.780	0.840	0.820	1.030	1.040	1.060	1.010
blbt4sa	10	-0.11	n/s	0.14	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.026	0.028	0.032	0.034
					Velocity	0.105	0.149	0.146	0.181	0.216	0.183	0.182	0.158	0.142	0.056
blbt4sb	10	0.15	n/s	2.60	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.025	0.030	0.040	0.050
					Velocity	0.067	0.043	0.103	0.033	0.050	0.047	0.069	0.056	0.071	0.142
blbt4sc	10	0.77	**	31.30	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.090	0.120	0.140
					Velocity	0.470	0.230	0.590	0.480	0.480	0.560	0.730	0.780	0.860	0.800
blbt5sa	10	0.79	**	34.70	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.035	0.040	0.050
					Velocity	0.257	0.276	0.340	0.297	0.300	0.326	0.360	0.380	0.400	0.370
blbt5sb	10	0.68	*	20.20	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	0.060
					Velocity	0.169	0.283	0.289	0.310	0.291	0.294	0.294	0.310	0.420	0.420
blbt5sc	10	0.87	***	61.61	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.100	0.140	0.160

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.189	0.202	0.254	0.233	0.239	0.251	0.410	0.400	0.410	0.370
blbt6sa	10	0.82	**	42.70	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.050	0.070	0.090
					Velocity	0.269	0.360	0.264	0.278	0.251	0.340	0.460	0.460	0.530	0.580
blbt6sb	10	0.80	**	37.50	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	0.060
					Velocity	0.470	0.580	0.520	0.530	0.530	0.560	0.580	0.620	0.690	0.680
blbt6sc	10	0.76	**	29.80	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.050	0.070	0.090
					Velocity	0.060	0.427	0.500	0.530	0.550	0.460	0.650	0.720	0.890	0.820
blbt7sa	10	-0.08	n/s	0.32	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.025	0.030	0.040	0.050
					Velocity	0.297	0.220	0.237	0.243	0.282	0.234	0.201	0.226	0.292	0.293
blbt7sb	10	0.92	***	108.40	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.100
					Velocity	0.142	0.152	0.263	0.240	0.370	0.280	0.470	0.530	0.640	0.570
blbt7sc	10	0.76	**	29.79	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.026	0.028	0.030
					Velocity	0.490	0.610	0.680	0.710	0.760	0.740	0.670	0.790	0.850	0.920

Table III – 2, Duneaton Water data. Depth (m) are heights above the bed. Velocity (ms^{-1}) are 50 second averages. Sample codes are first two letters = site, third letter is section a or b, the number refers to the transect and the last two letters designate the sample along the transect. Eighteen (36 %) out of fifty two velocity profiles were non-significant. Eight invertebrate samples did not have velocity profiles taken with them at this site, this usually occurred where water velocity was not detectable, i.e. in the shallows.

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
duat1sa	7	0.30	n/s	4.99	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.050	0.060	0.080
					Velocity	0.000	0.011	0.007	0.004	0.007	0.017	0.035	0.026	0.040	0.006
duat1sb	10	-0.05	n/s	0.59	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.150	0.220	0.280
					Velocity	0.025	0.310	0.059	0.053	0.076	0.056	0.082	0.074	0.076	0.023
duat1sc	10	0.90	***	84.28	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.140	0.180	0.220
					Velocity	0.025	0.029	0.022	0.037	0.044	0.036	0.050	0.074	0.069	0.072
duat2sa	10	0.83	**	45.92	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.280	0.360
					Velocity	0.092	0.096	0.102	0.112	0.114	0.075	0.122	0.185	0.208	0.194
duat2sb	10	0.07	n/s	1.65	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.070	0.090	0.120
					Velocity	0.002	0.031	0.023	0.017	0.020	0.018	0.022	0.023	0.026	0.024
duat2sc	10	-1.23	n/s	0.01	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.090
					Velocity	0.013	0.012	0.009	0.006	0.010	0.026	0.006	0.016	0.009	0.012
duat3sa	10	0.84	**	50.10	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.380
					Velocity	0.076	0.082	0.099	0.087	0.108	0.124	0.125	0.152	0.147	0.155
duat3sb	10	-0.05	n/s	0.57	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.200	0.260
					Velocity	0.019	0.005	0.010	0.020	0.014	0.031	0.014	0.013	0.019	0.024
duat3sc	10	-0.03	n/s	0.75	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.090

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.005	0.008	0.014	0.028	0.028	0.019	0.015	0.014	0.006	0.006
duat4sa	10	0.80	**	36.97	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.420
					Velocity	0.086	0.077	0.060	0.068	0.082	0.088	0.087	0.131	0.162	0.177
duat4sb	10	0.88	***	67.86	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.410
					Velocity	0.063	0.069	0.096	0.112	0.047	0.119	0.178	0.205	0.203	0.213
duat4sc	10	-0.01	n/s	0.93	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.120	0.180	0.240
					Velocity	0.148	0.031	0.024	0.024	0.023	0.038	0.029	0.031	0.036	0.028
duat5sa	10	0.69	*	20.86	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.150	0.220	0.310
					Velocity	0.004	0.019	0.014	0.005	0.017	0.004	0.021	0.050	0.031	0.042
duat5sb	10	0.88	***	68.96	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.210
					Velocity	0.008	0.013	0.013	0.018	0.025	0.013	0.030	0.048	0.052	0.043
duat5sc	8	0.10	n/s	1.78	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.023	0.026		
					Velocity	0.002	0.006	0.007	0.010	0.064	0.007	0.013	0.039		
duat6sa	10	0.50	5	10.30	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.440
					Velocity	0.044	0.074	0.081	0.072	0.079	0.046	0.152	0.106	0.095	0.132
duat7sa	10	0.96	***	231.08	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.150	0.300	0.400	0.480
					Velocity	0.103	0.086	0.104	0.080	0.136	0.117	0.215	0.274	0.313	0.304
duat7sb	10	0.01	n/s	1.08	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.150
					Velocity	0.007	0.006	0.009	0.010	0.013	0.012	0.013	0.011	0.004	0.004
duat8sa	10	0.95	***	183.32	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.140	0.200	0.260
					Velocity	0.118	0.121	0.140	0.120	0.154	0.128	0.163	0.239	0.279	0.299

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
duat9sa	10	0.19	n/s	3.16	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.070	0.150	0.230	0.300
					Velocity	0.013	0.031	0.021	0.021	0.030	0.035	0.037	0.038	0.031	0.029
duat9sb	10	0.95	***	174.30	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.200
					Velocity	0.098	0.100	0.105	0.129	0.143	0.148	0.194	0.259	0.294	0.380
duat10sa	10	0.94	***	143.48	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.160
					Velocity	0.196	0.203	0.214	0.230	0.213	0.266	0.297	0.310	0.390	0.420
duat10sb	9	0.87	**	52.53	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.090	0.130	
					Velocity	0.262	0.270	0.315	0.260	0.302	0.313	0.327	0.400	0.430	
duat10sc	10	0.91	***	88.42	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.050	0.065	0.080
					Velocity	0.149	0.144	0.151	0.172	0.168	0.165	0.186	0.194	0.228	0.245
dubt1sa	10	0.87	***	64.09	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.160	0.240	0.320
					Velocity	0.131	0.122	0.146	0.171	0.147	0.146	0.223	0.273	0.253	0.236
dubt1sb	10	0.33	5	5.35	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.045	0.060	0.070
					Velocity	0.165	0.176	0.189	0.178	0.309	0.190	0.228	0.255	0.265	0.248
dubt1sc	10	0.20	n/s	3.29	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.022	0.024	0.026	0.028
					Velocity	0.108	0.102	0.102	0.090	0.130	0.103	0.131	0.123	0.125	0.114
dubt2sa	10	0.29	n/s	4.76	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.110	0.170	0.220
					Velocity	0.229	0.191	0.088	0.204	0.146	0.400	0.440	0.370	0.262	0.390
dubt2sb	10	0.70	*	22.21	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.090	0.180	0.270	0.350
					Velocity	0.183	0.059	0.170	0.088	0.090	0.149	0.197	0.226	0.310	0.310
dubt2sc	10	0.27	n/s	4.28	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.028	0.032	0.038

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.109	0.139	0.157	0.163	0.162	0.162	0.166	0.146	0.176	0.152
dubt3sa	10	0.44	n/s	1.41	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.090	0.130	0.180
					Velocity	0.180	0.222	0.215	0.208	0.214	0.218	0.172	0.185	0.219	0.289
dubt3sb	10	0.86	***	56.33	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.110	0.160	0.220
					Velocity	0.142	0.153	0.179	0.222	0.219	0.221	0.249	0.272	0.380	0.430
dubt3sc	10	-0.11	n/s	0.13	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.022	0.024	0.026	0.028
					Velocity	0.026	0.048	0.050	0.046	0.047	0.500	0.042	0.059	0.044	0.040
dubt4sa	10	0.86	***	56.91	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.070	0.130	0.190	0.260
					Velocity	0.112	0.131	0.182	0.157	0.172	0.117	0.234	0.296	0.470	0.480
dubt4sb	10	0.82	**	42.84	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.090	0.140	0.180
					Velocity	0.294	0.349	0.370	0.330	0.340	0.370	0.350	0.460	0.480	0.490
dubt4sc	10	0.18	n/s	3.05	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.028	0.032	0.035
					Velocity	0.064	0.097	0.097	0.081	0.081	0.091	0.088	0.088	0.131	0.091
dubt5sa	10	0.82	**	42.57	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.200
					Velocity	0.006	0.007	0.010	0.016	0.016	0.016	0.028	0.137	0.280	0.320
dubt5sb	10	0.95	***	164.64	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.200
					Velocity	0.250	0.270	0.340	0.309	0.323	0.350	0.430	0.500	0.640	0.590
dubt5sc	10	0.54	*	11.53	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.024	0.028	0.032	0.036
					Velocity	0.009	0.017	0.018	0.018	0.020	0.016	0.021	0.024	0.018	0.035
dubt6sa	10	0.97	***	293.93	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.190
					Velocity	0.049	0.071	0.082	0.095	0.120	0.187	0.260	0.510	0.600	0.590

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
dubt6sb	10	0.73	*	25.23	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.080	0.110	0.140
					Velocity	0.600	0.620	0.610	0.650	0.640	0.650	0.670	0.730	0.680	0.690
dubt6sc	10	0.73	*	25.23	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.050	0.065	0.080
					Velocity	0.289	0.290	0.300	0.272	0.295	0.302	0.320	0.310	0.370	0.390
dubt7sa	10	-0.02	n/s	0.80	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.060	0.075	0.090
					Velocity	0.079	0.109	0.129	0.155	0.122	0.172	0.165	0.098	0.078	0.237
dubt7sb	10	0.00	n/s	1.01	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.120	0.180	0.240
					Velocity	0.066	0.093	0.089	0.049	0.040	0.080	0.089	0.092	0.098	0.068
dubt7sc	10	0.67	*	19.00	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.120	0.180	0.240
					Velocity	0.330	0.350	0.340	0.340	0.400	0.430	0.520	0.680	0.680	0.470
dubt8sa	10	0.87	***	61.46	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.110
					Velocity	0.007	0.007	0.025	0.125	0.212	0.270	0.389	0.320	0.460	0.490
dubt8sb	10	0.95	***	178.88	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.080	0.110	0.130
					Velocity	0.290	0.274	0.390	0.410	0.490	0.570	0.680	0.790	0.850	0.870
dubt9sa	10	0.46	5	8.59	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.050	0.070	0.090
					Velocity	0.480	0.540	0.560	0.580	0.550	0.540	0.560	0.600	0.590	0.580
dubt9sb	10	0.94	***	145.79	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.035	0.060	0.080	0.100
					Velocity	0.254	0.370	0.440	0.420	0.440	0.430	0.490	0.720	0.790	0.830
dubt9sc	10	0.70	*	21.88	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.110
					Velocity	0.540	0.580	0.570	0.610	0.600	0.590	0.630	0.680	0.670	0.630
dubt10sa	10	0.90	***	83.72	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.190

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
dubt10sb	10	0.86	***	65.64	Velocity	0.226	0.200	0.251	0.253	0.273	0.300	0.280	0.410	0.440	0.440
					Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.060	0.090	0.120
					Velocity	0.047	0.059	0.056	0.081	0.056	0.076	0.057	0.166	0.207	0.278

Table III – 3, River Etive data. Depth (m) are heights above the bed. Velocity (ms^{-1}) are 50 second averages. Sample codes are first two letters = site, third letter is section a or b, the number refers to the transect and the last two letters designate the sample along the transect. Twenty two (44 %) out of forty nine velocity profiles were non-significant. Eleven invertebrate samples did not have velocity profiles taken with them at this site, this usually occurred where water velocity was not detectable, i.e. in the shallows.

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
etat1sc	10	0.35	5	5.81	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.160	0.200
					Velocity	0.110	0.145	0.137	0.148	0.138	0.138	0.130	0.129	0.159	0.179
etat2sa	10	0.44	5	8.19	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.160
					Velocity	0.047	0.029	0.039	0.033	0.037	0.025	0.013	0.061	0.107	0.075
etat2sb	6	-0.1	n/s	0.16	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.150	0.250	0.350
					Velocity	0.087	0.109	0.144	0.116	0.136	0.138	0.113	0.080	0.033	0.258
etat2sc	10	0.89	***	73.39	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.380
					Velocity	0.050	0.040	0.062	0.061	0.068	0.071	0.083	0.133	0.115	0.129
etat3sa	10	0.82	**	41.50	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.150
					Velocity	0.079	0.097	0.117	0.118	0.107	0.119	0.122	0.140	0.154	0.148
etat3sb	10	0.83	**	45.57	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.200	0.300	0.380
					Velocity	0.054	0.065	0.045	0.080	0.095	0.105	0.142	0.133	0.254	0.233
etat3sc	10	0.91	***	96.68	Depth	0.010	0.014	0.018	0.022	0.026	0.030	0.200	0.400	0.600	0.760
					Velocity	0.041	0.027	0.057	0.087	0.072	0.056	0.136	0.208	0.183	0.180
etat4sb	3	-0.11	n/s	0.19	Depth	0.010	0.020	0.030	0.040	0.045	0.300	0.600	0.700	0.870	
					Velocity	0.071	0.091	0.145	0.062	0.147	0.025	0.053	0.019	0.343	
etat4sc	4	0.31	5	5.11	Depth	0.010	0.015	0.020	0.025	0.030	0.035	0.200	0.400	0.600	0.650

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.138	0.196	0.206	0.295	0.276	0.280	0.274	0.277	0.266	0.297
etat5sa	10	0.8	**	37.33	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.250	0.450	0.550
					Velocity	0.012	0.057	0.044	0.065	0.049	0.090	0.202	0.160	0.213	0.223
etat5sb	10	0.84	**	47.65	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.250	0.450	0.550
					Velocity	0.042	0.050	0.057	0.056	0.023	0.049	0.075	0.090	0.158	0.160
etat5sc	10	0.93	***	119.83	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.160	0.220	0.280
					Velocity	0.040	0.035	0.040	0.040	0.041	0.070	0.108	0.131	0.191	0.186
etat6sa	5	0.15	n/s	2.69	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.200
					Velocity	0.048	0.008	0.027	0.042	0.033	0.057	0.046	0.046	0.040	0.063
etat6sb	10	0.27	n/s	4.42	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.150	0.300	0.450	0.520
					Velocity	0.011	0.036	0.020	0.013	0.008	0.006	0.025	0.007	0.056	0.162
etat6sc	10	0.75	**	27.31	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.150	0.250	0.300
					Velocity	0.033	0.008	0.006	0.006	0.013	0.025	0.013	0.055	0.127	0.130
etat7sb	10	0.21	n/s	3.39	Depth	0.010	0.020	0.030	0.040	0.050	0.060	0.200	0.400	0.600	0.740
					Velocity	0.066	0.052	0.065	0.082	0.076	0.094	0.083	0.065	0.079	0.106
etat7sc	10	-0.05	n/s	0.58	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.150	0.200	0.300
					Velocity	0.069	0.029	0.049	0.073	0.047	0.062	0.041	0.049	0.046	0.051
etat8sa	10	0.69	*	21.17	Depth	0.010	0.013	0.016	0.019	0.022	0.025	0.150	0.300	0.450	0.520
					Velocity	0.070	0.044	0.028	0.059	0.031	0.057	0.069	0.104	0.102	0.109
etat8sb	6	-0.07	n/s	0.33	Depth	0.010	0.013	0.016	0.019	0.022	0.025	0.100	0.200	0.300	0.480
					Velocity	0.010	0.011	0.021	0.027	0.025	0.026	0.030	0.022	0.006	0.012

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
etat8sc	5	0.27	n/s	4.37	Depth	0.010	0.015	0.020	0.025	0.030	0.035	0.150	0.300	0.450	0.580
					Velocity	0.034	0.049	0.038	0.067	0.069	0.060	0.058	0.059	0.082	0.060
etat9sc	6	-0.1	n/s	0.15	Depth	0.010	0.012	0.014	0.016	0.180	0.020	0.040	0.080	0.012	0.016
					Velocity	0.065	0.048	0.044	0.064	0.072	0.073	0.064	0.057	0.074	0.080
etat10sc		0.67	5	11.55	Depth	0.010	0.012	0.014	0.016	0.018	0.020				
					Velocity	0.164	0.311	0.314	0.333	0.345	0.356				
etbt1sb	10	0.72	*	24.21	Depth	0.010	0.014	0.018	0.022	0.026	0.030	0.100	0.200	0.300	0.380
					Velocity	0.241	0.314	0.191	0.229	0.384	0.390	0.340	0.470	0.780	0.670
etbt1sc	6	0	n/s	0.33	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.100	0.150	0.200	0.300
					Velocity	0.164	0.311	0.314	0.333	0.345	0.356	0.363	0.360	0.390	0.261
etbt2sa	10	-0.04	n/s	0.65	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.180	0.240
					Velocity	0.287	0.640	0.680	0.710	0.570	0.390	0.690	0.710	0.600	0.571
etbt2sb	10	0.6	*	14.61	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.180
					Velocity	0.096	0.117	0.131	0.142	0.137	0.139	0.183	0.117	0.472	0.503
etbt2sc	10	0.43	5	7.90	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.180	0.220
					Velocity	0.133	0.061	0.098	0.176	0.112	0.040	0.106	0.123	0.560	1.700
etbt3sa	10	0.65	*	17.93	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.160	0.240	0.360
					Velocity	0.019	0.145	0.219	0.139	0.136	0.143	0.212	0.338	0.350	0.256
etbt3sb	10	0.35	5	5.90	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.200
					Velocity	0.490	0.630	0.420	0.620	0.199	0.550	0.550	0.590	0.760	0.860
etbt3sc	10	0.67	*	19.70	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.070	0.120	0.170	0.220

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
					Velocity	0.071	0.266	0.203	0.094	0.286	0.287	0.570	0.660	1.360	0.630
etbt4sb	10	0.51	5	10.47	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.160	0.240
					Velocity	0.191	0.264	0.225	0.266	0.230	0.273	0.275	0.291	0.277	0.307
etbt4sc	10	0.38	5	6.57	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.200	0.300
					Velocity	0.470	0.490	0.530	0.500	0.560	0.580	0.550	0.600	0.680	0.540
etbt5sa	6	0.26	n/s	4.20	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.180
					Velocity	0.035	0.082	0.068	0.131	0.080	0.123	0.118	0.118	0.502	0.113
etbt5sb	10	-0.02	n/s	0.84	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.120	0.160
					Velocity	0.620	0.667	0.780	0.730	0.750	0.850	0.820	0.640	0.690	0.610
etbt5sc	6	-0.1	n/s	0.13	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.100	0.120
					Velocity	0.730	0.660	0.700	0.660	0.610	0.590	0.670	0.670	0.680	0.640
etbt6sa	6	-0.09	n/s	0.20	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	0.070
					Velocity	0.283	0.208	0.421	0.307	0.240	0.750	0.208	0.441	0.560	0.249
etbt6sb	10	0.54	*	11.70	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.140	0.200	0.260
					Velocity	0.250	0.335	0.326	0.370	0.340	0.254	0.450	0.480	0.520	0.370
etbt6sc	10	0.19	n/s	3.12	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.040	0.050	0.070
					Velocity	0.450	0.123	0.080	0.123	0.336	0.303	0.330	0.136	0.513	0.587
etbt7sa	10	0.53	*	11.30	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.025	0.030	0.035	0.040
					Velocity	0.132	0.220	0.244	0.254	0.201	0.222	0.215	0.238	0.293	0.375
etbt7sc	6	0.21	n/s	3.41	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.030	0.060	0.090	0.120
					Velocity	0.530	0.510	0.550	0.540	0.530	0.560	0.540	0.530	0.550	0.570

Sample	Number of points	Pearson's Rsq adj	P value	F statistic											
etbt8sa	10	0.48	5	9.54	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.080	0.012	0.016
					Velocity	0.083	0.103	0.042	0.042	0.073	0.135	0.137	0.208	0.101	0.017
etbt8sb	10	-0.04	n/s	0.61	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.100
					Velocity	0.163	0.316	0.425	0.476	0.491	0.497	0.475	0.492	0.391	0.354
etbt8sc	10	0.51	5	10.52	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.050	0.100	0.150	0.180
					Velocity	0.142	0.130	0.143	0.197	0.191	0.196	0.188	0.221	0.674	0.372
etbt9sb	9	-0.12	n/s	0.01	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.100
					Velocity	1.165	0.097	0.113	0.158	0.133	0.106	0.187	0.255	0.540	0.499
etbt9sc	10	0.94	***	158.10	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.120	0.240	0.320
					Velocity	0.082	0.120	0.170	0.159	0.199	0.270	0.393	0.600	0.880	0.780
etbt10sa	6	0.23	n/s	3.71	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.060	0.100	0.120	0.180
					Velocity	0.039	0.183	0.182	0.224	0.124	0.370	0.325	0.127	0.139	1.990
etbt10sb	6	-0.1	n/s	0.16	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.040	0.060	0.080	0.100
					Velocity	0.299	0.233	0.233	0.299	0.265	0.325	0.226	0.308	0.205	0.358
etbt10sc	10	0.1	n/s	2.06	Depth	0.010	0.012	0.014	0.016	0.018	0.020	0.080	0.160	0.240	0.300
					Velocity	0.035	0.014	0.060	0.031	0.028	0.025	0.096	0.056	0.062	0.033

Appendix IV: TWINSPAN ordered species by samples tables

Introduction

The results of the TWINSPAN analyses used in chapters 2 and 3, is presented here as order species by samples tables. Taxon (OTU) codes are used throughout. The full taxon names are given in table 2-5,chapter 2. In each matrix a and b refer to the deep and shallow sections respectively. The last column and last row give the cuts produced by TWINSPAN. These are represented as ones and zeros, the line of binary digits closest to the rest of the matrix represents the first cut. The numbers in the matrix are pseudospecies counts. Pseudospecies are a representation of the species abundance in simplified form, (Jongman 1988) .

For all sites TWINSPAN failed to make a clear destination between samples from deep and shallow sections.

Table IV-1, River Etive data. The first major split is identified by using bold text to separate the two groups.

```
           a b b b b a a a b b b b a a a a a b a b a a a b b b b b b b b b a b a a b b b b b b b b a a b b b b b b b
Epig       3 - - - - - 1 2 2 1 1 - - 1 - - - - - - - 2 2 2 3 - 1 - - 2 1 2 - 2 1 1 - - - - - - - - - - - - - - - - 0
Hept       2 4 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 0
Pebi       - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 0
Hydr       - - - - 1 1 2 1 1 2 4 4 4 3 3 4 3 4 - - - 2 4 - - 4 - 1 - 4 - 1 - - 2 - - - - - - - - - - - - - - - - - 1
Oxyt       - - 1 - - - - - - 4 - - - - - 3 1 1 - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - 1
Pofl       1 - 1 1 - - - 1 1 - - - - 1 - 1 - - - - - - 1 - - - - 2 - - - 2 - - - - - - - 1 - - - - - - - - - - - - 1
Rhse       - - - - - - - - - 1 - - - - - - - - - - - - - 1 - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - 1
Dyti       - - - - - - - - - - - - - 1 - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1
Para       - - 1 - - - 1 1 - - 1 - - - - - - - - - - 1 - 1 - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - 1
Nilo       - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1
Macro      - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1
Thien      - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - 1
Tany       - - - - - - - 2 - - - - - - - - - 2 - - 1 1 - - - - 1 1 - 1 1 - - - - - - - - - - - - - - - - - - - - - 1
Heter      - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1
Plco       - - 1 - - - - - - - - - - - - - - - - - - - - - - 2 - - - - - - - - - - - - - - - - - - - - - - - - - - 10
Calu       - - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - 11
Ecdy       - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - 1 - - - - - - - - - - - - - 11
Siar       - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - 11
lemo       - - - - - - - - - - - - - - - - - - 1 - 1 1 - - - 1 - 1 - - - - - - - - - - - - - - - - - - - - - - - - 11
Pemi       - - - - - - - - - - - - - - - - - - - - - - - - - - 2 - - - - - - - - - - - - - - - - - - - - - - - - - 11
Lob scur - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - 11
Ortho      - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 11
Virga      - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - 11
Diam       - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - 1 - - - - - - - - - - - - - - - - - - - - - - - 11
Genus II - - - - - - - - - - - - - - - - - - - - - - 2 - - - - - - - - - - - - - 2 - - - - - - - - - - - - - - - - 11
Cari       1 4 - - - - - - - - - - - - - - - - - - - - - - 2 - - 1 - - - - - - - 1 - - 1 1 - - - - - - - 1 - - - - 1
Olig       1 1 - - - - - - - - - 1 - 1 2 - - - - - - 1 2 1 - 2 - - 1 - - 4 3 - 4 2 - - - 1 - - - - - 1 - - - - - - 1
Barh       - - - - - - - - - 1 - - - 2 - - 1 - - - 1 1 - - 2 2 1 1 1 2 - 3 - - - 2 3 2 2 2 - - 2 - - - - - - - - - 1
Triss      - - - - - - - - - - - - - - - - - - - 1 - - 1 1 2 1 - - - 1 - - - - - - - - - - - - - - - 1 - - - - - - 1
Cric       - - - - - - - - - - - - - - - - 1 - - - 1 - 2 1 1 1 - 1 4 4 - - - - - 1 - - - - - - - 1 1 - 1 - - - 1 - 1
Poki       - - 1 - - - - - - - - - - 1 - - - - - - - - 1 - - 1 - - - - - - - - - - - - 1 1 - - - - - 1 - - - - - - 10
Tipu       - - - - - 1 - 1 - - 1 - - - 1 - 1 - - - 1 - 1 1 1 - - - - - - 1 1 1 - 1 - - 1 - - - - - 2 2 - - - - - - 10
Livo       - - - - - - - - - - - - 1 - - - - - - - 1 - 1 2 - 2 2 1 - 1 - 4 - - 1 - - - 2 1 - - - - 2 - - - 2 1 - 4 110
Ouli       - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - 1 - - - 110
Rise       - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - 2 1 - 1110
Simu       - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - 1 - 1 - 1110
Abla       - - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - 1 - - - - - - - 1110
Tven       - - - - - - - - - 1 - - - - - - - - - - - - - 1 - 2 - - 1 - - - - - - - - - - - 1 1 1 - 1 1 1 - - - - - 1110
Rheo       - - 2 - - - - - - 1 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - 1 - - 1 - - - - 1111

           0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1
           0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 1 1 1 1
               0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 1
               0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 0 0 1 1 1 1
                   0 0 0 0 0 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1
```

Table IV- 2, Blane Water data. The first major split is identified by using bold text to separate the two groups.

	a	b	b	a	a	b	b	a	b	b	b	b	b	a	b	b	b	b	b	b	b	b	b	b	b	a	a	a	b	b	b	b	b	b	b	a	a	b	b	a	b	a	**a**	**a**	**a**	**b**	**b**	**a**	**a**	**a**	**b**	**b**	**b**	
Livo	-	-	2	2	2	-	4	-	-	-	3	-	-	-	3	3	2	-	3	2	2	-	-	-	-	1	-	1	-	-	-	-	-	3	2	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	**1**	-	-	0
anfl	3	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
Lege	-	-	2	-	-	-	-	2	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Lefu	1	-	2	1	-	-	3	-	-	-	-	4	4	-	1	-	-	-	3	-	-	2	2	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Lemo	-	-	4	4	3	4	4	2	3	1	-	-	4	3	4	3	1	3	2	-	1	4	4	2	3	2	-	2	2	1	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	11
Rhdo	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Basc	-	-	-	-	2	-	-	1	-	1	-	-	2	-	1	-	-	-	-	2	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Simu	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3	1	1	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Hydro	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	-	1	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
Pemi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Glbo	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Barh	-	-	-	1	-	-	-	-	-	-	-	2	1	-	-	3	3	2	4	4	2	3	3	-	-	-	2	2	-	3	2	2	-	2	-	-	-	-	3	-	1	1	-	-	-	-	-	-	-	-	-	**1**	-	101
Ecdy	-	-	-	-	-	-	4	4	4	4	4	4	3	4	4	4	4	3	4	4	3	3	2	4	4	3	1	3	4	4	4	3	4	3	3	2	-	2	2	-	3	3	**1**	-	-	-	-	-	-	-	-	-	-	101
Outr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Lum	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Agmu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Gapu	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	1	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	11
Epig	-	-	-	-	-	-	4	4	2	4	2	4	4	4	4	2	2	4	4	4	2	4	2	2	3	3	3	4	4	2	4	1	2	2	1	4	1	2	4	3	2	3	**4**	**1**	**2**	-	-	**1**	-	-	-	-	**1**	1
Espa	-	-	-	1	1	-	1	1	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**	-	-	-	-	-	-	1

	a	b	b	a	a	b	b	a	b	b	b	b	b	a	b	b	b	b	b	b	b	b	b	b	b	a	a	a	b	b	b	b	b	b	b	a	a	b	b	a	b	a	**a**	**a**	**a**	**b**	**b**	**a**	**a**	**a**	**b**	**b**	**b**	
Tipu	2	2	4	3	4	-	1	-	2	3	3	-	3	4	4	1	4	3	2	3	3	2	4	4	1	1	-	1	1	1	-	2	2	2	-	2	-	1	2	1	1	1	**2**	**2**	**1**	**1**	-	-	-	-	-	-	-	1
Anne	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	**1**	-	-	-	**1**	-	-	-	-	10
Chir	-	3	4	-	2	-	3	-	-	-	-	-	4	4	4	2	1	4	4	3	1	3	2	2	1	-	1	1	2	-	1	-	-	2	-	4	-	2	3	4	2	4	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	-	-	10
Olig	2	-	2	1	-	-	-	-	-	-	-	-	1	2	-	2	-	1	1	1	-	-	-	1	1	-	1	-	1	-	3	2	1	1	1	-	-	-	1	2	2	3	**3**	-	**2**	**2**	**1**	-	**1**	-	-	-	-	10
Hir	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	1	1	-	-	**2**	-	**1**	-	**1**	-	-	-	-	10
Suc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**	**1**	11
Lehi	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	11
Outu	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	**2**	**2**	-	-	**3**	**2**	**3**	-	-	**2**	**3**	11
Hydra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	**2**	**2**	-	-	-	-	-	-	-	-	-	11
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	
	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	

Table IV-3, Duneaton Water data. The first major split is identified by *using bold text* to separate the two groups.

	a	b	b	a	a	b	b	a	b	b	b	b	b	a	b	b	b	b	b	b	b	b	b	b	b	a	a	a	b	b	b	b	b	b	b	a	a	b	b	a	b	a	**a**	**a**	**a**	**b**	**b**	**a**	**a**	**a**	**b**	**b**	**b**	
Livo	-	-	2	2	2	-	4	-	-	-	3	-	-	-	3	3	2	-	3	2	2	-	-	-	-	1	-	1	-	-	-	-	-	3	2	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	**1**	-	-	0
anfl	3	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
Lege	-	-	2	-	-	-	-	2	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Lefu	1	-	2	1	-	-	3	-	-	-	-	4	4	-	1	-	-	-	3	-	-	2	2	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Lemo	-	-	4	4	3	4	4	2	3	1	-	-	4	3	4	3	1	3	2	-	1	4	4	2	3	2	-	2	2	1	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	11
Rhdo	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Basc	-	-	-	-	2	-	-	1	-	1	-	-	2	-	1	-	-	-	-	2	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Simu	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3	1	1	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Hydro	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	-	1	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
Pemi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Glbo	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Barh	-	-	-	1	-	-	-	-	-	-	-	2	1	-	-	3	3	2	4	4	2	3	3	-	-	-	2	2	-	3	2	2	-	2	-	-	-	-	3	-	1	1	-	-	-	-	-	-	-	-	-	**1**	-	101
Ecdy	-	-	-	-	-	-	4	4	4	4	4	4	3	4	4	4	4	3	4	4	3	3	2	4	4	3	1	3	4	4	4	3	4	3	3	2	-	2	2	-	3	3	**1**	-	-	-	-	-	-	-	-	-	-	101
Outr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Lum	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101
Agmu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Gapu	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	1	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	11
Epig	-	-	-	-	-	-	4	4	2	4	2	4	4	4	4	2	2	4	4	4	2	4	2	2	3	3	3	4	4	2	4	1	2	2	1	4	1	2	4	3	2	3	**4**	**1**	**2**	-	-	**1**	-	-	-	-	**1**	1
Espa	-	-	-	1	1	-	1	1	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**	-	-	-	-	-	-	1
Tipu	2	2	4	3	4	-	1	-	2	3	3	-	3	4	4	1	4	3	2	3	3	2	4	4	1	1	-	1	1	1	-	2	2	2	-	2	-	1	2	1	1	1	**2**	**2**	**1**	**1**	-	-	-	-	-	-	-	1
Anne	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	**1**	-	-	-	**1**	-	-	-	-	10
Chir	-	3	4	-	2	-	3	-	-	-	-	-	4	4	4	2	1	4	4	3	1	3	2	2	1	-	1	1	2	-	1	-	-	2	-	4	-	2	3	4	2	4	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	-	-	10
Olig	2	-	2	1	-	-	-	-	-	-	-	-	1	2	-	2	-	1	1	1	-	-	-	1	1	-	1	-	1	-	3	2	1	1	1	-	-	-	1	2	2	3	**3**	-	**2**	**2**	**1**	-	**1**	-	-	-	-	10
Hir	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	1	1	-	-	**2**	-	**1**	-	**1**	-	-	-	-	10
Suc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**	**1**	11
Lehi	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	11
Outu	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	**2**	**2**	-	-	**3**	**2**	**3**	-	-	**2**	**3**	11
Hydra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	**2**	**2**	-	-	-	-	-	-	-	-	-	11
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	
	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	
	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**			
		0	0	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1			**0**	**0**	**1**	**1**	**1**	**1**	**1**			
							0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1					**0**	**0**	**0**	**1**	**1**			

Appendix V: Individual responses of benthic invertebrates to velocity, depth and substrate.

Introduction

The raw data for the analyses presented in chapter 4 are given below. For each site there is a table giving each taxon's log abundance and the corresponding values of flow variables. Each row represents a sample. There is a second table for each site giving the results of the gaussian curve fitting.

Table V-1, River Etive data. As the abundance data is log transformed zeros are presented.

Hydroptila	*Polycentropus flavomaculatus*	*Polycentropus*	*Baetis rhodani*	*Caenis rivulorum*	*Ephemerella ignita*	*Tanypodinae*	*Orthocladiinae*	Chironominae	Tipulidae	Oligochaeta	*Limnius volckmari*	Substrate	Velocity m/s	Depth m
0.00	0.69	0.69	1.79		0.69				0.00	2.64	2.83	37	0.21	0.08
1.10			0.00		0.00			0.00				256	0.06	0.18
	0.00	0.69				1.10		1.79				61.6	0.11	0.4
1.95					0.00	0.00			0.00			231	0.14	0.16
2.40										0.00		256	0.16	0.79
									0.00	1.79		1	0.00	0.18
1.95											0.00	256	0.29	0.89
					1.10				0.00			164.2	0.18	0.55
	0.00	0.00		0.00	1.61					0.00		37	0.12	0.58
1.79	0.00	0.69	0.69		0.00					0.00		90.75	0.13	0.3
1.39							0.00	0.00	0.00	0.69		212.2	0.06	0.55
0.69			0.00		1.10	0.69		0.00		0.00		37	0.08	0.34
1.10					0.00	0.00		0.00		2.94	0.00	37	0.01	0.2
2.30	0.00	0.00										234.1	0.08	0.76
2.20	0.00	0.69			1.10	0.69	1.39	0.00	0.00	1.10	0.00	73.9	0.05	0.33
0.00									0.00			123.1	0.09	0.55
0.69					0.00	0.00		0.00				37	0.07	0.52
0.00	0.00	0.00			0.69	0.00		0.69	0.00			58.4	0.13	0.61
						0.00	0.69	0.00	1.10		0.69	6	0.04	0.03
1.79			0.00				0.00		0.00			256	0.12	0.11
					0.69	0.69	1.10		0.00	0.00	1.10	158.8	0.39	0.4
			1.39									123.1	0.77	0.2
			0.69									256	0.09	0.25
			0.69	0.69	1.61	0.69			0.00			98.5	0.27	0.38
											0.69	208	0.66	0.22
		0.00				0.00	0.00		0.69	0.00		73.9	0.07	0.23
0.00	0.00	0.00			1.10	0.00						234.1	0.29	0.28
2.30		0.00	0.69				1.10			0.69	0.69	37	0.26	0.2
							1.10					256	0.12	0.17
			0.69				0.00					256	0.68	0.08
			0.00		0.00						0.69	147.7	0.42	0.28
0.00	0.69	0.69	0.00	0.00			0.00	0.00			0.00	160	0.23	0.05
											2.64	256	0.59	0.14
			0.69	0.00	0.00		1.39		0.00	1.10		61.6	0.43	0.12
			0.00			0.00	2.08	0.00		0.00		256	0.34	0.2
		0.00	0.69	0.00					0.00		0.69	73.9	0.02	0.09
2.20			0.69		1.10	0.00	2.40	0.00			0.00	256	0.35	0.11
				1.95						0.00		73.9	0.64	0.38
	0.00	0.69	1.10	0.00			0.69	0.00		0.00	0.00	73.9	0.68	0.19

Table V-2. River Etive, gaussian curve fitting , regression results. Significant p values are in bold. Where the value of p appears as 0 it is less than 0.001.

	Hydroptila	*Polycentropus flavomaculatus*	*Polycentropus*	*Baetis rhodani*	*Caenis rivulorum*	*Ephemerella ignita*	Tanypodinae	Orthocladiinae	Chironominae	Tipulidae	Oligochaeta	*Limnius volckmari*
Velocity												
Fstatistic	0.50	1.82	0.07	1.87	0.86	3.22	0.00	1.12	0.26	0.87	1.18	0.24
P value	0.62	0.22	0.93	0.19	0.48	0.07	1.00	0.35	0.78	0.44	0.34	0.79
R squared adjusted	-0.06	0.14	-0.17	0.09	-0.04	0.21	-0.15	0.01	-0.12	-0.02	0.02	-0.11
b0	1.73	-0.26	0.28	0.45	-0.08	-0.19	0.26	0.07	0.13	0.31	1.26	0.34
b1	-8.89	3.69	-0.08	-0.60	0.94	10.54	-0.25	4.62	1.06	-2.18	-3.98	1.48
b2	25.70	-5.10	0.39	2.02	0.71	-22.27	0.49	-6.13	-2.06	3.45	3.51	-1.11
Depth												
Fstatistic	1.06	20.78	1.01	0.23	2.07	1.26	3.90	0.44	0.68	1.52	3.44	0.38
P value	0.37	**0.00**	0.40	0.80	0.22	0.31	**0.05**	0.65	0.53	0.26	0.06	0.69
R squared adjusted	0.01	0.80	0.00	-0.10	0.23	0.03	0.28	-0.07	-0.05	0.06	0.25	-0.09
b0	1.57	0.83	0.46	0.76	-0.89	0.31	-0.53	0.35	-0.22	0.48	2.57	0.95
b1	-3.52	-3.75	-0.31	-1.41	10.02	0.25	5.08	3.52	2.28	-2.53	-9.55	-1.83
b2	4.67	3.69	-0.45	1.08	-13.89	1.61	-6.53	-7.49	-2.38	3.04	8.49	0.91
Substrate												
Fstatistic	1.06	0.15	2.54	0.88	0.36	0.06	2.87	0.58	0.60	1.26	2.61	0.27
P value	0.37	0.87	0.12	0.43	0.71	0.94	0.09	0.57	0.57	0.32	0.11	0.77
R squared adjusted	0.01	-0.21	0.19	-0.14	-0.22	-0.12	0.20	-0.05	-0.06	0.03	0.18	-0.11
b0	1.37	0.01	-0.27	0.65	-1.16	0.45	0.01	1.25	0.01	0.36	1.89	0.89
b1	-0.01	0.00	0.01	0.00	0.03	0.00	0.01	-0.01	0.01	0.00	-0.02	-0.01
b2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table V-3, Duneaton Water data. As the abundance data is log transformed zeros are presented.

Leuctra	*Ancylus fluviatilis*	*Hydropsyche*	*Baetis*	*Ephemerella ignita*	*Ecdyonurus*	*Limnius volckmari*	*Oulimnius tuberculatus*	Chironomidae	Tipulidae	Oligochaeta	Velocity ms^{-1}	Depth m	Substrate
								3.91			0.019	0.09	1
				1.61				3.74	0.00	0.69	0.068	0.28	43.1
			0.00				1.10				0.059	0.24	6.6
1.39				1.79	3.00		0.00	0.00	0.00	0.00	0.167	0.38	41.35
			0.00	0.69	1.39			0.69	0.00	0.69	0.023	0.13	51.85
							1.61	3.30		0.00	0.012	0.1	49.75
								1.39	1.10		0.138	0.39	27.7
				0.00			1.61				0.019	0.27	19
				0.00	1.61	0.69	0.69			0.00	0.134	0.43	26.2
1.10				1.39	1.61	0.00			0.00		0.183	0.42	49.3
				0.69				2.94	0.00	0.69	0.031	0.25	19
				1.95	1.10			2.40	1.10		0.032	0.32	19
				0.00							0.039	0.22	19
			0.69	1.61	0.00			0.00		0.00	0.112	0.45	98.5
				0.00			0.69	3.37			0.025	0.2	19
1.61			0.00	2.64	2.83						0.248	0.49	37
							1.39	3.22		0.00	0.007	0.15	19
1.39				3.33	3.00			3.00	2.48	1.10	0.233	0.27	37
				2.08	0.00		1.10		0.69	1.39	0.007	0.05	19
0.00			0.00	1.39	1.39			3.37	0.00	1.39	0.032	0.31	19
2.20	0.69		0.00			0.69			1.61	0.00	0.257	0.21	37
				0.00			0.69	3.95	1.10		0.193	0.09	30.8
0.00	1.39								1.10	1.10	0.331	0.17	73.9
0.69	1.79		0.69	2.83	1.79	0.00		0.00	0.00		0.380	0.19	98.5
1.39			0.69			0.69		0.69	2.71		0.193	0.09	30.8
2.64			1.10	2.08	3.14		0.00				0.229	0.33	98.5
2.30			0.00	2.08	4.17	1.61		2.08	2.40		0.230	0.08	37
0.69		0.00		2.40	2.40			1.10	0.00	0.00	0.329	0.23	160
0.00			1.61	1.10	2.20				0.00		0.241	0.36	35.95

Leuctra	*Ancylus fluviatilis*	*Hydropsyche*	*Baetis*	*Ephemerella ignita*	*Ecdyonurus*	*Limnius volckmari*	*Oulimnius tuberculatus*	Chironomidae	Tipulidae	Oligochaeta	Velocity ms^{-1}	Depth m	Substrate
						0.00		2.48			0.146	0.04	26.2
								1.95	0.00	1.10	0.222	0.19	72.8
1.61				0.69	1.95				1.10		0.315	0.23	135.4
1.79			1.39	0.69	1.95	1.39		0.69	0.00	0.69	0.064	0.03	37
0.00			0.00	2.08	2.40				1.61		0.339	0.27	61.6
0.00	0.00		1.39	1.10	2.83	1.10		0.00	1.95		0.429	0.19	49.3
2.08											0.088	0.045	37
0.00	0.00		1.10	2.08	2.56			0.00		1.39	0.169	0.21	31.3
0.00	0.00	0.69	0.69	0.00	1.61				0.69	0.69	0.039	0.22	98.5
0.00				1.10	2.30	1.61			1.61		0.016	0.04	61.6
0.69	0.00			1.10	2.20				0.69	0.00	0.419	0.2	98.5
1.39		0.00	0.69	3.71	1.61		1.95	3.71	1.39	0.00	0.676	0.15	98.5
2.64	0.00			2.40	3.04	1.95		1.39	0.00		0.327	0.09	98.5
				0.69	0.69	0.00		0.69	0.00		0.141	0.1	19
			1.39	2.40	0.69	0.00		1.61	0.69	0.00	0.008	0.16	160
2.20		0.00	2.20	2.48	1.95	1.79		2.20	1.10	0.00	0.544	0.25	98.5
		1.10	2.64	2.20	1.95	1.10		1.39	1.39	0.00	0.332	0.12	123.1
2.77		0.00				0.69		2.20	2.20	0.69	0.687	0.14	147.7
0.00			0.69	0.69	1.79	0.69		0.00	1.79		0.111	0.06	80
2.30		0.00	1.79	2.64	1.61			1.39	0.69		0.570	0.1	110.8
			0.69	1.10	1.61	1.61		0.69	1.10	0.00	0.617	0.11	160
2.48			1.79	0.69	0.69			0.69	2.20		0.632	0.12	98.5
3.22			1.39	2.71	1.79			2.30	1.39	0.00	0.159	0.13	234.1
0.69			0.00	1.10	2.30			0.69	2.56	0.00	0.036	0.02	19

Table V-4. Duneaton Water data, gaussian curve fitting , regression results. Significant p values are in bold.

	Leuctra	*Ancylus fluviatilis*	*Hydropsyche*	*Baetis*	*Ephemerella ignita*	*Ecdyonurus*	*Limnius volckmari*	*Oulimnius tuberculatus*	Chironomidae	Tipulidae	Oligochaeta
Velocity											
Fstatistic	1.9	0.52	1.629	2.245	4.542	8.482	0.794	13.441	3.276	1.45	0.662
P value	0.168	0.623	0.304	0.129	**0.017**	**0.001**	0.47	**0.003**	**0.05**	0.248	0.525
R squared adjusted	0.057	-0.159	0.173	0.091	0.1505	0.306	-0.025	0.71	0.115	0.0231	-0.027
b0	0.80	-0.53	0.76	0.41	0.85	1.03	0.59	1.42	2.62	0.78	0.55
b1	1.35	8.67	-0.60	2.38	4.50	8.87	0.98	-8.55	-8.94	0.27	-0.63
b2	0.77	-15.07	-0.90	-1.42	-3.98	-13.23	0.12	13.79	12.16	1.37	0.10
Depth											
Fstatistic	0.446	1.627	0.078	0.591	0.067	0.147	0.586	2.172	1.715	2.504	0.495
P value	0.645	0.286	0.927	0.562	0.935	0.864	0.569	0.176	0.196	0.096	0.615
R squared adjusted	-0.038	0.152	-0.444	-0.034	-0.049	-0.053	-0.051	0.19	0.039	0.073	-0.4
b0	1.73	-6.13	-0.27	0.75	1.34	1.68	1.09	1.16	0.71	1.46	0.21
b1	-3.98	96.74	7.93	2.51	1.27	2.47	-1.36	2.17	13.41	-2.24	2.79
b2	5.95	-315.95	-25.80	-7.16	-1.80	-4.52	-0.47	-10.51	-31.25	-1.58	-6.65
Substrate											
Fstatistic	3.104	0.3807	0.697	5.022	3.403	0.253	1.293	0.136	2.708	0.0517	2.435
P value	0.061	0.701	0.55	0.160	0.437	0.778	0.303	0.875	0.081	0.95	0.109
R squared adjusted	0.123	-0.215	-0.112	0.243	0.107	-0.046	0.033	-0.209	0.088	-0.053	0.099
b0	0.92	-2.02	-8.44	-0.05	0.83	1.92	-0.03	1.33	2.77	1.00	0.78
b1	0.00	0.08	0.14	0.02	0.01	0.00	0.03	-0.02	-0.03	0.00	-0.01
b2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table V-5, Blane Water data. As the abundance data is log transformed zeros are presented.

Ephemerella ignita	*Ecdyonurus*	*Baetis rhodani*	*Leuctra*	*Ancylus fluviatilis*	*Glossoma Boltoni*	*Agaptus*	*Oulimnius*	*Limnius volckmari*	*Elmis aenea*	Velocity ms^{-1}	Depth m	Substrate
4.48	1.79		1.79	0.00			0.00	0.00		0.415	0.12	
	2.48	0.69	0.00		0.00			1.10	0.00	1.533	0.24	
4.39	1.39		1.39				1.10		0.00	1.069	0.19	39
4.37	1.79		1.39			0.00	2.20	1.61	0.69	0.000	0.00	43
								0.00	0.00	0.000		30
3.58	1.39		1.39				0.00	0.00	0.00	0.378	0.19	43
			3.33	1.10			0.69	0.69		0.549	0.32	35
3.87	1.10	0.00								0.603	0.29	38
2.94	1.95		0.69					0.00	0.00	0.195	0.09	45
3.00	0.69		1.95							0.133	0.04	36
			0.00				1.39	2.40	1.10	0.080	0.09	34
3.14			1.39	0.00						0.318	0.23	35
3.33				0.00			1.61	1.61	0.00	0.345	0.16	20
2.89	0.00		2.40		0.00		0.69			0.323	0.22	74
2.89	1.95		1.10	1.39			1.39	0.69	0.69	0.228	0.23	0
										0.135	0.07	10
2.08	1.79						1.10	0.00	0.69	0.528	0.14	28
			0.00	1.10						0.345	0.21	24
2.40				0.00				1.79	1.39	0.223	0.16	13
2.77	1.10		0.00					0.00		0.300	0.24	67
3.50	1.79	0.00					0.00	0.00		0.000	0.00	62
4.28	3.14	1.95	0.00				1.39			0.219	0.03	54
3.95	1.61	2.77		3.00	2.48	0.69	2.08	2.08	1.95	0.550	0.18	86

Ephemerella ignita	*Ecdyonurus*	*Baetis rhodani*	*Leuctra*	*Ancylus fluviatilis*	*Glossoma Boltoni*	*Agaptus*	*Oulimnius*	*Limnius volckmari*	*Elmis aenea*	Velocity ms^{-1}	Depth m	Substrate
			0.69	0.69	2.64	1.10	1.10	2.20	1.39	0.751	0.19	43
4.57	1.10	1.61	0.69				0.00			0.065	0.10	42
1.10			1.39		1.39		0.69	2.94	1.10	0.930	0.13	43
			2.71	0.69			1.39	0.00	0.69	0.393	0.06	46
3.43		1.61	2.56	0.00	2.08			0.00		0.882	0.14	28
			2.64		1.95			0.69		0.949	0.17	62
1.39			1.61					0.00		0.125	0.34	25
3.81	2.56	0.00		0.00	1.79		0.00	0.00	0.69	0.064	0.05	41
4.54	1.61	1.95	1.39	2.30	2.20	1.39		2.48	0.00	0.683	0.14	49
1.79			1.61	1.10	0.69	0.00	0.69	0.00	0.00	0.333	0.06	37
3.26	1.10		1.79				1.61	0.69	1.61	0.313	0.06	37
3.50	2.20		2.89				0.69			0.384	0.07	37
3.83	2.08	0.00	1.79	0.00	0.69	0.00	2.20	2.20	1.95	0.589	0.07	37
3.64	0.00	0.00			0.69					0.662	0.10	28
0.69							0.00			0.253	0.06	25
1.79	0.00		1.39				0.00	0.00	0.69	0.451	0.11	49
3.74	1.39						1.61	1.39	2.30	0.654	0.04	37

Table V-6. Blane Water data, gaussian curve fitting , regression results. Significant p values are in bold.

	Ephemerella ignita	*Ecdyonurus*	*Baetis rhodani*	*Leuctra*	*Ancylus fluviatilis*	*Glossoma Boltoni*	*Agaptus*	*Oulimnius*	*Limnius volckmari*	*Elmis aenea*
Velocity										
Fstatistic	1.02	0.68	2.44	1.46	2.56	0.81	1.85	0.38	1.57	0.49
P value	0.38	0.52	0.16	0.25	0.12	0.48	0.30	0.69	0.23	0.62
R squared adjusted	0.00	-0.31	0.24	0.04	0.19	-0.40	0.25	-0.06	0.04	-0.05
b0	2.45	1.96	-1.43	1.07	-0.16	0.35	-0.55	0.85	0.49	0.41
b1	0.02	-0.01	0.04	0.00	0.03	0.01	0.01	0.00	0.00	0.01
b2	0.20	-0.69	1.28	1.06	0.10	1.22	1.52	0.49	1.23	0.35
Depth										
Fstatistic	1.19	1.08	1.75	0.65	7.37	0.26	3.35	0.06	0.06	0.95
P value	0.32	0.36	0.24	0.94	**0.01**	0.78	0.17	0.94	0.94	0.41
R squared adjusted	0.01	0.01	0.14	-0.08	0.49	0.06	0.48	-0.09	-0.09	-0.01
b0	3.16	1.84	0.05	1.34	-0.33	1.00	-0.12	0.98	0.98	0.91
b1	-2.21	-2.94	1.81	0.78	3.37	4.30	7.69	-0.44	-0.67	-2.41
b2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate										
Fstatistic	0.67	0.91	0.12	0.13	0.40	0.28	3.79	0.27	0.92	0.75
P value	0.52	0.42	0.99	0.88	0.68	0.76	0.15	0.77	0.41	0.49
R squared adjusted	0.05	-0.01	-0.25	-0.07	-0.09	-0.15	0.53	-0.07	-0.01	0.08
b0	3.28	1.57	1.01	1.42	0.40	1.63	-0.16	0.89	0.89	1.04
b1	0.38	0.40	0.01	-0.16	0.54	-0.32	1.40	0.42	0.50	-0.07
b2	-7.30	-8.66	-2.19	2.06	7.53	-2.36	16.83	-2.09	-5.30	-10.50