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The influence of hydrogeology and the Devensian glaciation on hyporheic communities of the UK

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The influence of hydrogeology and the Devensian glaciation on hyporheic communities of the UK

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A thesis submitted in partial fulfilment of the requirements for the degree of PhD

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Abstract

Ecologically, the hyporheic zone (HZ) performs numerous roles within stream ecosystems (e.g. habitat, refugia from floods and droughts, nutrient cycling, pollution attenuation) with the dominant control on these various roles sediment composition. Recently, the body of literature on the role of sediment in the HZ has grown, though these studies rarely extend beyond the reach scale with little regional scale research undertaken in England and Wales. In this thesis, meio- and macrofaunal hyporheic assemblages at two depths (20cm and 50cm) across four geological regions (chalk – fine sediment, sandstone - fine to medium sediment and limestone – coarse sediment) two seasons (summer (n = 396) and winter (n = 192)) are described. The influence of recent glaciations (Devensian) on the distribution of stygobite fauna (summer (n = 192) and winter (n = 98)) is also considered. A reach scale experimental manipulation of sediment composition in the HZ of a highly dynamic, species rich and diverse study site (limestone) was also undertaken. I found the influence of glaciation on stygobite fauna still apparent in the two limestone areas with macrofaunal sized stygobite species rare or absent in both limestone areas. Meiofaunal sized stygobite fauna *Antrobathynella stammeri* (Crustacea: Syncarida) were recorded from the glaciated limestone site. These results suggest large stygobite fauna are rare or absent in the limestone areas of Northern England with meiofaunal stygobites possibly surviving in sub-glacial refugia. Stygobite fauna were abundant in southern England with alternative migratory routes north discussed (e.g. River Severn catchment and chalk aquifers). Geological regions had characteristic fauna with species richness and abundance of meio- and macrofauna high in the HZ of both limestone areas. Conversely, species richness and abundance was low in the chalk and sandstone HZ. The chalk HZ had a high abundance of macrofaunal sized Crustacea (*Gammarus pulex*) and low abundance of meiofaunal sized Crustacea (Copepoda). This suggested mechanical properties (burrowing) rather than morphology (body size and shape) was important in fine sediments, whereas in the limestone HZ morphology rather than mechanical properties was important. In the experimental study results were more intuitive with meiofauna abundant across all sediment treatments (fine, mixed, coarse and natural) with macrofauna abundant in sediment treatments containing a high proportion of coarse material. These results suggest Copepoda assume a greater role in ecological processes in fine sediment patches within a dynamic HZ, whereas when fine sediment dominates a system (e.g. chalk HZ) then the role of Copepoda is reduced. One implication could be the use of Copepoda as indicators of colmation and hydrologic exchange in the assessment of ecosystem health and give an indication of the refugial capacity of the HZ from projected high and low flow events in light of UK climate change forecasts.

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Chapter I: The influence of climate and hydrogeology on the hyporheos of groundwater dominated streams in the UK

General introduction

Recent advances in freshwater ecology and the convergence of the disciplines of stream ecology and groundwater ecology have greatly enhanced our understanding of rivers and their associated energy flows (Danielopol 1989, Petts and Amoros 1996, Jones and Mulholland 2000). At the interface between surface waters and groundwaters is the hyporheic zone, containing elements of both surfacewater and groundwater and measurable along lateral and vertical biological and chemical gradients (Williams 1989, Fraser and Williams 1998, Williams et al. 2010). The hyporheic zone is the main conduit between surface water and groundwater and is described by White (1993:62) as ‘the saturated interstices beneath the stream bed, and into the stream banks, that contain some proportion of channel water, or that have been altered by surface water infiltration’.

Until relatively recently the hyporheic zone was rarely studied as an integral component of aquatic ecosystems. Initial conceptual models of streams and rivers, for example, the River Continuum Concept and Flood Pulse Concept failed to include a vertical dimension, though recently aquatic ecosystem theoretical models have become more inclusive (Thorp et al. 2006). The importance of the hyporheic zone to stream ecosystem processes has also been shown in numerous studies (Boulton et al. 1998, Fellows et al. 2001, Boulton and Hancock 2006). Ecosystem processes occurring within the hyporheic zone include: habitat and refugia for meio- and macrofauna (meiofauna retained on 63 μ m sieve and pass through 500 μ m sieve: macrofauna larger than 500 μ m); medium for nutrient cycling and also pollutant attenuation (biofilms) (Hester and Gooseff 2010).

Streams and rivers are complex entities with longitudinal, lateral and vertical fluxes of water, organic matter and nutrients with a temporal dimension adding further complexity (Junk et

al. 1989, Walker et al. 1995, Junk 1999). Longitudinal patterns (Fig. 1:1A) in habitat diversity along the course of rivers have served as a central theme in Stream Ecology (Vannote et al. 1980, Thorp and Delong 1994, Tockner and Ward 1999, Thorp and Delong 2002). The lateral dimension (Fig. 1:1B) connects the main river channel and the terrestrial environment, consisting of a complex gradient of aquatic and riparian habitats (Junk et al. 1989). The vertical dimension (Fig. 1:1C) connects groundwater to surfacewater with the hyporheic zone the primary ecotone between them (Brunke and Gonser 1997, Thorp et al. 2006). The temporal dimension also occurs across numerous scales, for example diurnally, annually and over longer time periods (climate change) (Ward 1989).

Regarding climate change, recent studies have shown the assemblage of fauna occupying the hyporheic zone (the hyporheos) to be influenced by flow permanence which increased hyporheic taxon richness, density and assemblage (Datry et al. 2007). Current predictions of climate change in the UK suggest wetter winters and drier summers (Hulme 2002) potentially affecting groundwater levels and associated river flows (Jackson et al. 2010) and subsequently the hyporheos and groundwater fauna. All these dimensions influence habitat quality and heterogeneity, with spatial heterogeneity in all dimensions within rivers and streams reflecting the structural diversity of the riverine landscape. The streambed-water interface is recognized as an integral component of river ecosystems exhibiting extensive heterogeneity across spatial (Schmid-Araya 1997, Fraser and Williams 1998) and temporal scales (Stanford and Ward 1993, Soulsby et al. 2009).

Historically, research on stream and rivers has been conducted by scientists in two main disciplines: Ecology and Geomorphology. Their approach differs even though describing similar systems (Harper et al. 1992). Freshwater ecologists commonly investigate from the 'top down' (e.g. the biota living in the river) to describe conditions within the system (Rosgen 1994, Holmes et al. 1998, Wright et al. 1998, Kemp et al. 1999). Geomorphologists on the other hand research using a 'bottom up' approach (i.e. landscape, geology, relief) to

describe conditions within the system (Stott 2010). In recent years, Geomorphologists have attached themselves to the growing field of ‘Ecohydrology’ (Le Clerc et al. 1996, Kemp et al. 2000, Newson and Newson 2000) which attempts to link knowledge from Hydrology, Geomorphology and Ecology to predict response of ecosystems to a range of abiotic factors (Hannah et al. 2004). Scientists working in the hyporheic environment have long been aware that biotic and abiotic factors are difficult to separate.

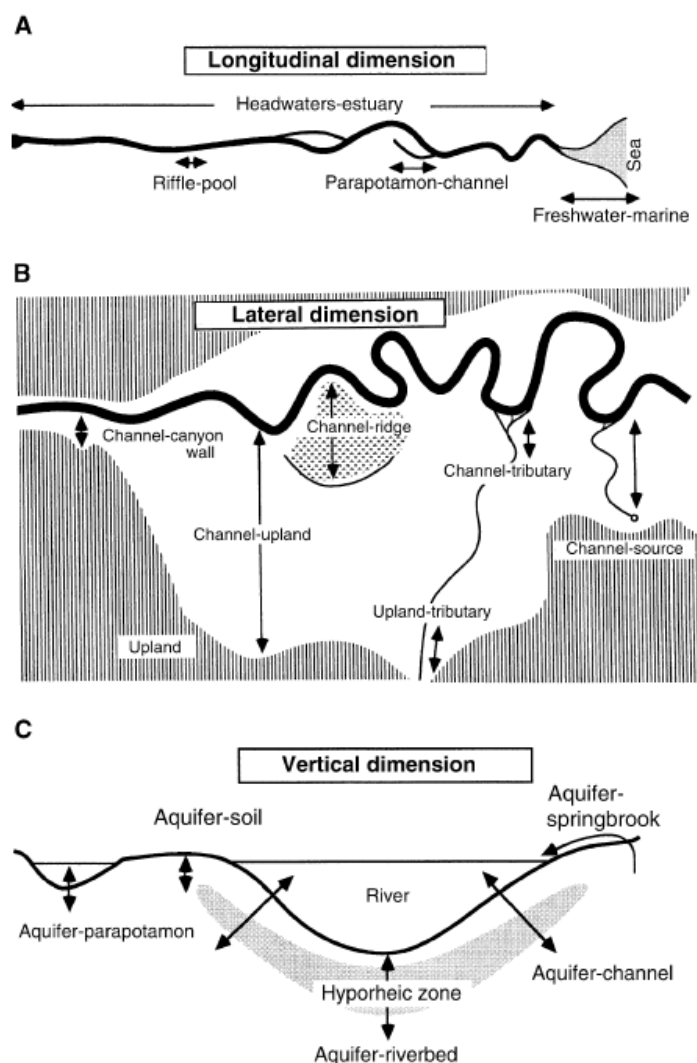


Figure 1:1. Major ecotones and pathways of exchange (arrows) of materials, energy, and organisms in the longitudinal (A), lateral (B), and vertical (C) dimensions of a riverine system (Ward and Wiens 2001).

The term hyporheic was first coined by Orghidan (1959) although as early as 1935 it had been recognised that invertebrate fauna were present in interstitial shallow alluvial sediments (Karaman 1935). The boundary between surfacewater and groundwater was first described by Schwoerbel (1961) although not until the development of minipiezometer methods by Lee and Cherry (1978) could field ecologists measure sub-surface flowpaths. This led to the realisation that sub-surface flowpaths and the hyporheos were connected with characteristic fauna found at up- and downwelling zones at the tail and head of riffles, respectively (Marmonier 1986). Epigeal fauna were associated with downwelling zones (riffle head) whereas hyporheic fauna were associated with upwelling zones (riffle tail) (Marmonier 1986).

The interstitial spaces of the hyporheic zone have long been known to provide a habitat for macro and meiofaunal taxa (Stanford and Gaufin 1974, Williams and Hynes 1974, Hynes 1983), though it was not until the 1990's that groundwater ecology gained global recognition with the 1st International Groundwater Ecology Symposium in 1992. The four dimensional nature of streams and rivers described by Ward (1989) is now an accepted part of stream ecosystem theory with the vertical dimension weighted equally with the lateral and longitudinal dimensions (Smock et al. 1992, Dole-Olivier 1998). Scale is also an important component in describing fluvial systems, with the hierarchical structure of streams at local, intermediate and regional scales first described by Tóth (1963) whose idealised model could also be conceptualised within a catchment scale model.

Table 1:1. Hierarchical organisation of a second or third order mountain stream with approximate spatial and temporal scales of patch sizes (Frissell et al. 1986).

Patch body	Spatial scale	Temporal scale
Microhabitat	10^{-1}	10^{-1} to 10^0
Pool/riffle	10^0	10^0 to 10^1
Reach	10^1	10^1 to 10^2
Segment	10^2	10^3 to 10^4
Catchment	10^3	10^5 to 10^6

The issue of scale was addressed by Frissell et al. (1986) who integrated both spatial and temporal elements (Table 1:1). At the microhabitat scale, leaf packs, gravel patches and other small patch types occur on a spatial scale of 10^{-1} metres and have a temporal persistence of 10^{-1} to 100 years. As spatial and temporal scales increase then influences on the riverine landscape change. Catchment scale landscape features evolve over long periods and are shaped by processes occurring up to 10^6 year timescales (e.g. glacial periods). During the 1990's, knowledge of the hyporheic zone evolved dramatically resulting in the proposal of ecosystem concepts such as the hyporheic corridor concept (Stanford and Ward 1993) and the fluvial hydrosystem concept (Petts and Amoros 1996). These ecosystem concepts utilise the hierarchical structure of drainage systems, describing the nested structure of rivers across a range of increasingly smaller, spatial and temporal scales.

Stanford and Ward (1993) proposed the hyporheic corridor concept which suggests three spatial scales associated with the hyporheic zone (Fig. 1:2). At the "sediment scale" microbial and chemical processes occur on sediment surfaces, creating microscale gradients. At the "reach scale" alternate up- and downwelling zones generate gradients in nutrients, dissolved gases and subsurface fauna across bedform features such as riffle-pool sequences. At the "catchment scale" a discontinuous pattern occurs as rivers flow from the headwaters to the sea. In the headwaters frequent up- and downwelling may occur within catchments which contain highly porous alluvial sediments. As the river increases in size the alluvial sediments decrease in size and hydraulic conductivity also decreases. This results in the dominant patterns of up- and downwelling changing as rivers increase in size (Heitmuller and Hudson 2009). Catchment scale up- and downwelling flow patterns are affected by changes in the valley width, depth of the bedrock, geology and local hydraulic head pressure. Stream water upwells as alluvial plains fan out and pressure decreases, stream water then downwells into the sub-surface as reaches begin to constrain and water pressure increases (Stanford and Ward 1993). Similarly the fluvial hydrosystem concept (Petts and Amoros

1996) describes rivers hierarchically. For example, the drainage basin would be the largest spatial unit with reaches nested within the drainage basin and described as a functional sector. Within river reaches are bedform features (e.g. pool-riffle features) described as functional units and within these units are mesohabitats. This model describes fluvial systems in three dimensions as described in Figure 1.1 with a temporal dimension also included in the model.

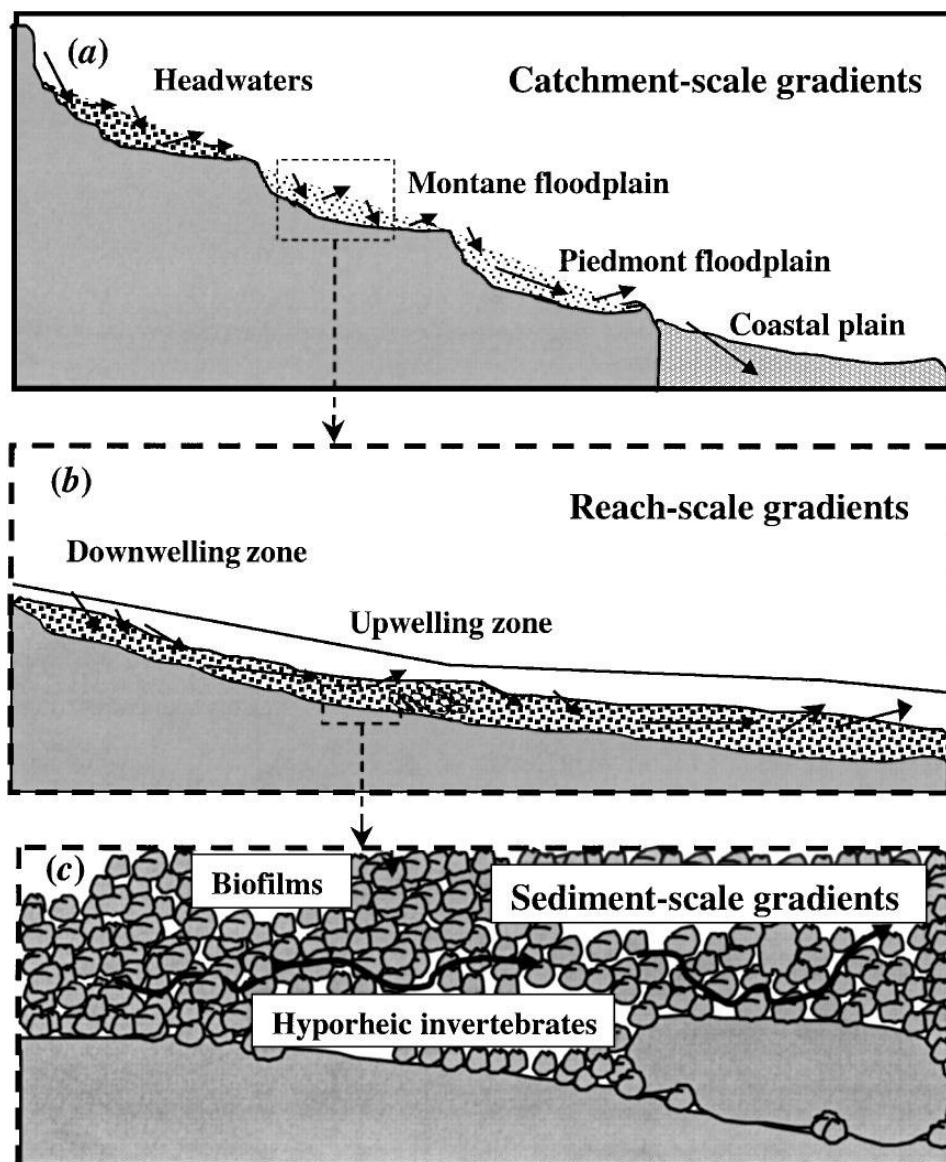


Figure 1:2 Diagrammatic representation of the processes described in the hyporheic corridor concept: (a), at the catchment scale a discontinuous pattern of upwelling and downwelling occurs. At the reach scale (b), alternate up- and downwelling zones generate gradients in nutrients, dissolved gases, and subsurface fauna. At the sediment scale (c), microbial and chemical processes occur on particle surfaces, creating microscale gradients. Arrows indicate water flow paths (Boulton et al. 1998).

One abiotic factor that should be mentioned in particular with reference to streams in the UK is the impact from river management and the modification of river channels. The River Habitat Survey of England and Wales revealed that channel form or substrate is significantly modified in approximately two-thirds of all surveyed sites (Raven et al. 1998) impacting processes in the hyporheic zone. For example, channel modification inhibits connectivity between surfacewater and groundwater with the removal of meanders to aid flood prevention also reducing vertical connectivity (Hester and Gooseff 2010).

In recent years, research into groundwaters and the hyporheic zone in Europe has received added impetus with the introduction of the European Union Water Framework Directive (WFD) and European Union Groundwater Directive (EU-WFD 2000). The WFD requires the UK Environment Agency to achieve good ecological status in surface water bodies by 2015. There is no direct mention of the hyporheic zone in the WFD, although the WFD does state that the management of groundwater and surfacewater should be conducted in an integrative manner. The WFD also states that if a surfacewater body fails to achieve good status due to interactions with groundwaters then the associated groundwater body will also fail to achieve good status. Pollution of surfacewater and groundwater bodies from agriculture and mine water pollution has been identified as one of the main risks in potentially failing to achieve a good ecological status by 2015 (Gandy et al. 2007). Biogeochemical attenuation processes in the hyporheic zone, in particular with regard to nitrate attenuation have been identified as an important component in helping to achieve WFD targets for UK water bodies (Gandy et al. 2007, Wexler et al. 2011). Groundwater and surfacewater systems are inextricably linked via the hyporheic zone with the management of groundwater and surfacewater requiring extensive knowledge of these systems.

In attempting to define the hyporheic zone it is necessary to include aspects of both surfacewater and groundwater environments with the hyporheic zone containing elements of

both and clearly distinct from adjacent surfacewater and groundwater (Brunke and Gonsler 1997). The hyporheic zone is described by Boulton et al., (1998) as a spatially fluctuating ecotone between surfacewater and groundwater, with the spatial scale of the ecotone changing both within and between catchments as local geology influences hydraulic conductivity.

Glacial influence on UK Rivers

In the UK glaciation has also had a major impact on many of the river systems with the effects of glaciations evident in many UK Rivers. Quaternary glaciations affected most of the UK with the Anglian glaciation (maximum extent 424 000 years BP) reaching as far south as Bristol and London and the most recent glacial event the Devensian glaciation (18 000 years BP) extending to the southern Pennines and the Welsh borders (Fig. 1:3). Glacial tills consist of a diverse range of sediment sizes from fine glacial clay deposits to stone blocks larger than a car (Creuze des Chatelliers et al. 1994). As glaciers retreat and outwash occurs the fine sediments are washed away leaving the larger, heavier sediments behind. These heavier sediment deposits are characterised by large grain sizes and a large area of interstitial space between the sediments providing opportunities for colonisation by fauna (Strayer 1994).

Many riverine landscapes have experienced cycles of change (aggradation – incision – aggradation) over the Quaternary period, related to changes in climate, vegetation cover, sediment sources and movement of sediment pulses (Shields et al. 2000, Macklin et al. 2006). The Quaternary glaciations affected much of northern Britain, while to the south of the glacier ice conditions were similar to Arctic climates of Canada and Northern Russia, with Quaternary glaciations driving dramatic changes in the landforms of the UK (Lewis et al. 2001, Clark et al. 2004). Rivers in the south of the UK, for example the Severn Basin were highly seasonal with low flows during the harsh cold winters followed by extreme flood events occurring during the spring thaw, with low flows again during the rest of the summer (Gregory 1997). The remaining large meandering valleys of the southern UK which

now only contain small streams are relicts from this time when river discharges were much greater than at present (Macklin and Lewin 2003, Macklin et al. 2010). There also remain valleys with no discernible river system, created by meltwater from the glacier ice, drainage from ice dammed lakes and surface runoff when precipitation was significantly higher (Clark et al. 2004). The river systems of the UK still contain large amounts of sediment laid down during the last period of Quaternary glaciations, with glacial materials still being released into the fluvial system (Gao et al. 2000).

Hydrogeology: influence of groundwater-surfacewater interactions on rivers in the UK

Groundwaters of the UK

Rivers and lakes are often groundwater fed with a large proportion of the water we use having spent some time in a groundwater aquifer, thus making the quality of groundwater important for drinking water, agriculture and industry. Groundwater is a vital resource playing a crucial role in supplying water to 75% of Europe's population (Petra 2009). Groundwater aquifers also contain more than 97% of the world's freshwater supply, not including frozen water (Hiscock 2007). The nature, mobility and quality of groundwater are dependent on the rock formations or aquifers in which groundwater is held. The primary physical factor of these rock formations is their porosity which determines the percentage of rock volume available to contain water (Hiscock 2007). The second important factor is the permeability of the rock formation determines how easily water can flow within the rock. High permeability is generally associated with high porosity, although clays have a low permeability although a large percentage of the interstitial space is filled with water (Hiscock 2007).

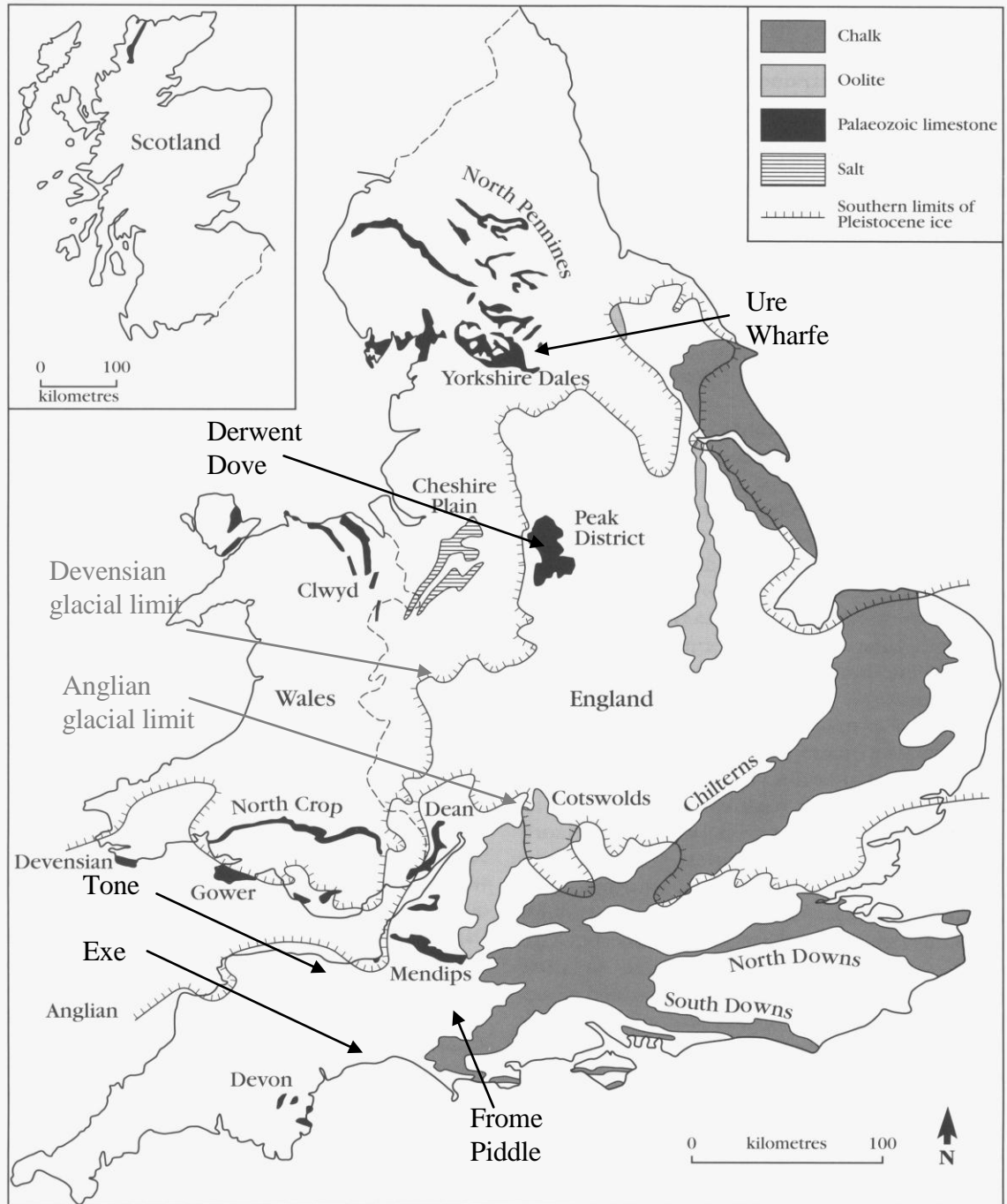


Figure 1:3. Map showing river locations chosen for the field survey. Ure and Wharfe rivers are located in the Yorkshire Dales on Carboniferous limestone; both rivers were glaciated during the Devensian glacial period. Dove and Derwent rivers are also on Carboniferous limestone and unglaciated during the Devensian glacial period. The Tone and Exe rivers are located on Permo-Triassic sandstone and the Frome and Piddle are located on Cretaceous chalk, all rivers unglaciated during the Devensian glacial period. The Devensian and Anglian glacial limit are indicated by the hatched side of line indicating the extent of glaciation (Waltham et al. 1997).

Rainfall and snowfall not lost to evaporation, transpiration or stream runoff will percolate through the soil and sediments into the groundwater (Fig. 1:4). Water percolating through soils and sediments is initially held tightly as a film on soil particle surfaces. As water moves

deeper down into the soil layers it collects on the surfaces of soil particles, air is still present in the void spaces in this unsaturated area (vadose zone). Moving deeper into the soil and sediment layers the interstitial spaces become filled with water producing a zone of saturation (phreatic zone), the upper level of which is the water table (Hiscock 2007).

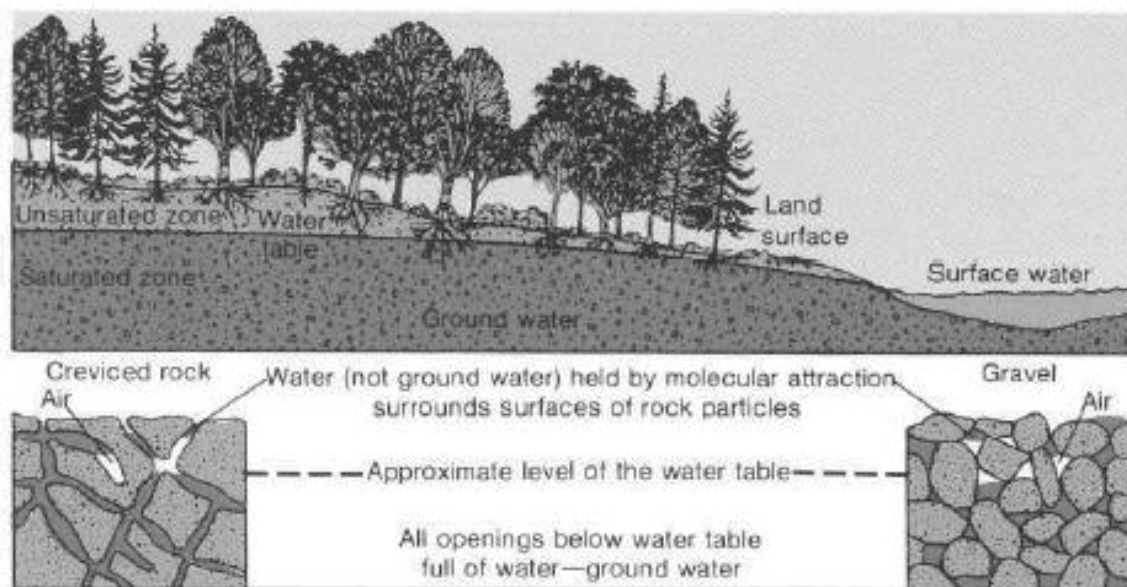


Figure 1:4. Water infiltration through the soil-water unsaturated zone and into the water table (Waller 2005).

In a series of landmark papers, Chebotarev (1955, 1956) stated that groundwaters follow a distinct salinity gradient with bicarbonate waters at the outcrop on the earth's surface to saline waters deep in the earth's crust. The water chemistry of groundwater is dependent on rock-water interactions and flow regimes across different hydrogeological environments giving groundwater and surfacewater their unique hydrochemical signature (Hanshaw and Back 1979). The chemical composition of groundwater is divided into major and minor ions, trace constituents and gases. In the aquatic environment the major ions, minor ions and dissolved gases contained in groundwater are shown in Table 1:2 with associated baseline concentration parameters.

Groundwater chemistry in the UK rarely conforms to natural baseline conditions (Shand et al. 2007) with many solutes derived from both natural and anthropogenic sources (e.g.

nitrate, phosphate, arsenic). In this study natural baseline conditions are defined following Shand et al (2007:4) as: “the range in concentration of an element, species or chemical substance present in solution which is derived by natural geological, biological, or atmospheric sources”. Groundwater recharge is from rainfall which in the atmosphere is exposed to atmospheric gases and particles released from power stations, cars and homes, leading to an increase in oxides of sulphur and nitrogen and a reduction of pH in many aquifers (Shand et al. 2007).

Recent concerns about groundwater quality in the UK have arisen particularly in regard to the increasing levels of nitrate in UK aquifers (Heathwaite et al. 1996, Rivett et al. 2007). Aquifers close to the earth’s surface are vulnerable to pollution from terrestrial sources for example, elevated nitrate levels in aquifers in the south and east of England generally coincide with the Chalk outcrops (Rivett et al. 2007). Levels of chemicals from agriculture have been increasing in unconfined aquifers for the last 40 years, with nitrate concentration close to or above the levels set for Drinking Water Guidelines for the UK (Shand et al. 2007). Unconfined aquifers by their very nature of being exposed to air at the earth’s surface are usually aerobic, therefore denitrification processes rarely occur with ion exchange not a dominant process (Shand et al. 2007). Concerns have also arisen regarding the quantity of supply, with high demand and restricted resource availability (Smakhtin 2001), particularly in the southern and eastern regions of England (Downing 1993, Lise and Bakker 2005). Groundwater protection in the UK has tended to develop with our knowledge and understanding of the implications of groundwater exploitation (Hiscock 2007). Impacts on groundwater will also affect surfacewater and subsequently the flora and fauna of surfacewater associated with the primary aquifers of the UK.

Table 1:2. Baseline chemical composition of groundwaters of the UK (Shand et al. 2007).

Groundwater composition		
Major ion (>5 mg L ⁻¹)		
Bicarbonate	Sodium	Chloride
Calcium	Sulphate	Magnesium
Minor ions (0.01 – 10.0 mg L ⁻¹)		
Nitrate	Potassium	Carbonate
Strontium	Fluoride	Iron
Phosphate	Boron	
Dissolve gases (trace to 10 mg L ⁻¹)		
Nitrogen	Methane	Oxygen
Hydrogen sulphide	Carbon dioxide	Nitrous oxide

Primary aquifers of the UK

The most important aquifers of the UK are found in the Cretaceous Chalk, Permo-Triassic Sandstone, Jurassic limestone and Lower Greensand strata. In the north and west of the UK, rocks are relatively impermeable and ancient (Pre-Cambrian and Palaeozoic) and less conducive to groundwater flow and storage (Shand et al. 2007). The major aquifers of the UK are located primarily in the permeable younger strata in southern and eastern England, occurring in the geological sequence of rocks ranging from the Permian to the Quaternary (Hiscock 2007). Aquifers do occur in ancient rock strata from the Devonian to the Carboniferous though these rocks are much harder with low permeability and therefore not as important for water supply. Ancient rock strata of the Silurian, Ordovician, Cambrian and Precambrian have low permeability although they can provide an impermeable basement for rocks of the Older and Younger Cover. The geology also has an impact on the climate (e.g. recharging of groundwater) with the generally older harder granitic rocks of the northwest having a higher relief and creating an orographic barrier which affecting rainfall (Douglas and Glasspoole 1947, Maraun et al. 2011) and consequently river flow through surface runoff (Leung et al. 2003) .

Cretaceous Chalk

Chalk is a soft white limestone underlying large areas of eastern and southern England and formed from marine sediment composed of minute calcareous shells (coccoliths) and other creatures with a carbonate skeleton. The groundwater in the chalk aquifer occurs in the fine pore spaces and fractures explaining chalks high porosity, these fine grains also increase the capillary action and reducing water flow within the aquifer with the specific yield (water a rock yields when it drains naturally or is pumped) approximately 1% (Hiscock 2007). The reason chalk is useful as an aquifer is due to the many large cracks and fissures within the chalk increasing the permeability, allowing water to flow more readily than if cracks and fissures were absent. There is an exchange and diffusion between the water in the pore spaces and water in the fractures, this has a strong influence on the groundwater chemistry over time as water moves through the aquifer (Edmunds et al. 2002).

Permo-Triassic sandstone

Permo-Triassic sandstone aquifers (PTS) are found in a series of deep sedimentary basins in western England, southwest England and on the eastern and western flanks of the Pennines. Thick sedimentary sequences of Permian and early Triassic sandy deposits form the PTS aquifers (Allen et al. 1997). The aquifer is highly permeable consisting of well-sorted fine to medium grained sands that are poorly cemented, contributing to a high specific yield of 20-25% with a high matrix porosity (20 to 30%) (Hiscock 2007) which releases a high proportion of the water stored within the aquifer (Edmunds et al. 2002). The PTS is classed as a major aquifer in Britain and is the second most important aquifer type in the UK, supplying approximately 25% of all licensed abstractions in England and Wales (Monkhouse and Richards 1982, Griffiths et al. 2002).

Limestone

The Jurassic limestone aquifers occur in eastern England and North Yorkshire and are composed of relatively hard rock which is enlarged through solution making them highly permeable. Wells in the Lincolnshire Limestone provide the highest yields in the UK with over 30 Ml/d^{-1} abstracted (Griffiths et al. 2006) with a specific yield of 14% (Hiscock 2007). The limestones of the Older Cover have a much longer history and were subjected to more intensive earth movements giving the rocks a lower porosity and permeability. The Carboniferous Limestone aquifers associated with the Older Cover are important with well-developed minor aquifers in the Peak District of Derbyshire, the Mendip Hills, north and south Wales and north-west Yorkshire (Allen et al. 1997).

Hydrogeological influences on hyporheic ecology

Groundwater-surfacewater interactions

Groundwater and surfacewater interact in a variety of ways depending on the hydrogeologic environment, with the scale of interactions influenced by topography, geology and climate (Tóth 1963, Toth 1970). Exchanges in the hyporheic zone are primarily determined by geomorphological and hydrological features of the river, such as variations in slope and depth, bed form features (i.e. riffle-pool sequences) and changes in flow direction (i.e. meanders, boulders) (Maddock et al. 1995, Brunke and Gonser 1997, Boulton et al. 1998, Pepin and Hauer 2002). In a riffle-pool sequence decreasing stream depth causes a high-pressure zone at the head of a riffle, resulting in surface water downwelling into the sediment (Fig. 1:5). Water can travel some distance beneath the riffle if conditions allow, as the depth of water increases at the tail of a riffle the water pressure will decrease and upwelling will occur (Boulton et al., 1998).

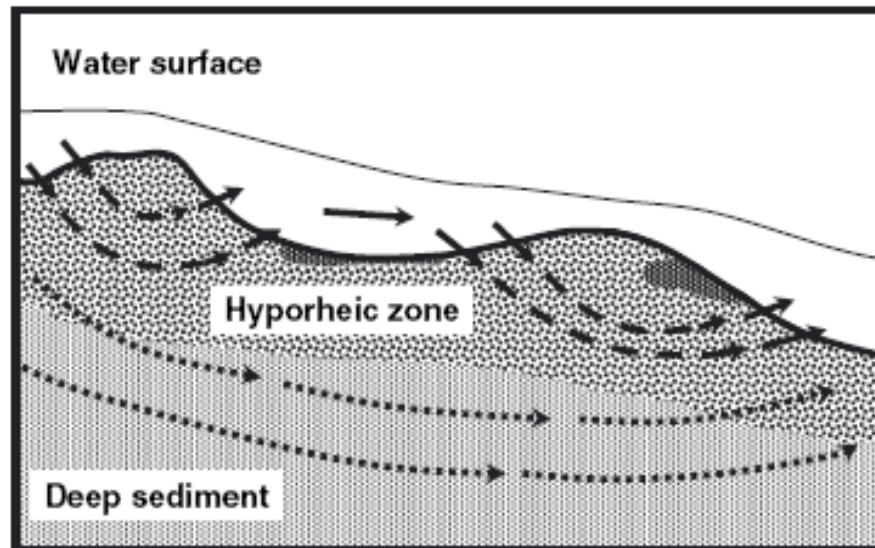


Figure 1:5. Longitudinal section of a hypothetical subsurface flow path through a riffle. Arrows indicate direction of flow. Flowpaths through coarse sediments are often shorter than flowpaths through fine sediments. Localised patches of fine sediments (fine stippling) at the surface can displace downwelling or upwelling zones, creating a mosaic of hydrological exchanges (Boulton et al. 1998).

Water flow in subsurface sediments is influenced by the local geology and consequently the alluvial sediments in the river bed. The characteristics of the catchment substrate will have a major impact on how precipitation enters the soil layers. Limestone, for example is highly permeable and water subsequently moves vertically downwards from the soil into the underlying aquifer. In contrast, catchments containing boulder clay runoff will occur as percolation rates are slower than rainfall rates, clay soils quickly become saturated leading to runoff and increased water levels in adjacent streams.

Hydraulic conductivity

The laws governing the flow of water in a saturated material can be described using Darcy's law which is written as:

$$\text{eq. 1. } Q = -KA \frac{dh}{dl}$$

where dh/dl represents the hydraulic gradient, the negative sign indicates flow always moves in the direction of decreasing hydraulic head. K is the hydraulic conductivity of the porous

material (e.g. alluvial sediments), while A is the cross-sectional area of flow. Fundamentally Darcy's law describes the ease of movement of water through alluvial sediments or hydraulic conductivity, which in nature spans 13 orders of magnitude (Table 1:3). In basic terms these orders of magnitude range from coarse grained materials with high hydraulic conductivity to fine grained materials displaying low hydraulic conductivity (Hiscock 2007). Penetration of surface waters longitudinally and vertically through bed form features will increase with steeper longitudinal hydraulic head gradients and coarser streambed sediments (Kasahara and Hill 2006, Tonina and Buffington 2007). Sediment size and in turn porosity has been found to affect the distribution and abundance of bacteria and invertebrates in subsurface sediments (Hunt and Stanley 2003, Navel et al. 2010, Taira and Tanida 2011) and hydrological retention is strongly influenced by the geology and alluvial characteristics of the catchment (Morrice et al. 1997).

Table 1:3. Ranges of values of hydraulic conductivities and porosity for different geological materials. Data taken from Hiscock (2007).

Geological material	Hydraulic conductivity K (m s^{-1})	Porosity, n
Alluvium	10^{-5} - 10^{-2}	0.05-0.35
Glacial deposits		
Basal till	10^{-11} - 10^{-6}	0.30-0.35
Lacustrine silt and clay	10^{-13} - 10^{-6}	0.35-0.70
Outwash sand and gravel	10^{-7} - 10^{-3}	0.25-0.50
Loess	10^{-11} - 10^{-5}	0.35-0.50
Sandstone	10^{-10} - 10^{-5}	0.05-0.35
Shales		
Unfractured	10^{-13} - 10^{-9}	0-0.10
Fractured	10^{-9} - 10^{-5}	0.05-0.50
Mudstone	10^{-12} - 10^{-10}	0.35-0.45
Dolomite	10^{-9} - 10^{-5}	0.001-0.20
Oolitic limestone	10^{-7} - 10^{-6}	0.01-0.25
Chalk		
Primary	10^{-8} - 10^{-5}	0.15-0.45
Secondary	10^{-5} - 10^{-3}	0.005-0.02
Coral limestones	10^{-3} - 10^{-1}	0.30-0.50
Karstified limestones	10^{-6} - 10^0	0.05-0.50
Marble, fractures	10^{-8} - 10^{-5}	0.001-0.02
Volcanic tuff	10^{-7} - 10^{-5}	0.15-0.40
Basaltic lava	10^{-13} - 10^{-2}	0-0.25
Igneous and metamorphic rocks:	10^{-13} - 10^{-5}	0-0.10
Fractured and unfractured		

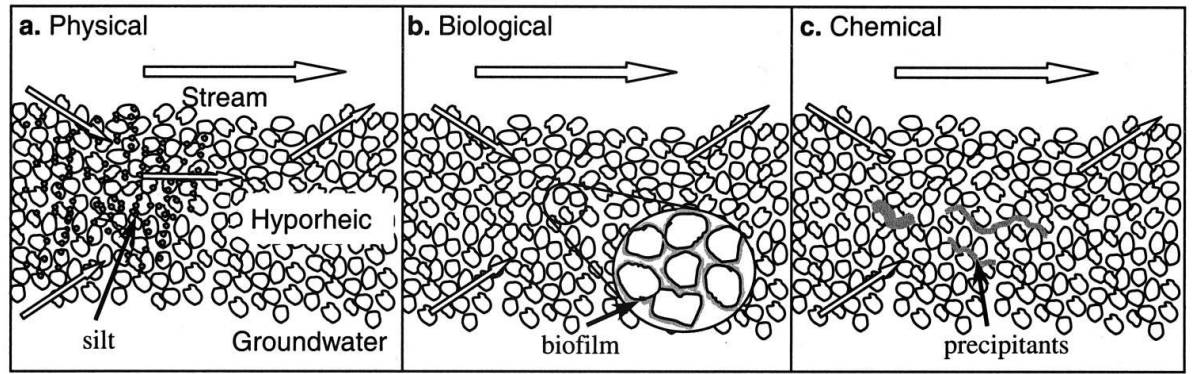


Figure 1:6 Three filtration processes that occur in the hyporheic zone: (a) physical filtration by the sediment matrix, (b) biological filtration by the microbial biofilm, and (c) chemical filtration by reactions such as mineral and redox processes (Hancock et al. 2005).

Headwater catchments of a given geological composition weather to produce alluvium of specific hydrogeological properties (e.g. sediment grain size, porosity, hydraulic conductivity) which affects the magnitude and occurrence of up- and downwelling along a stream (Morrice et al. 1997). Physicochemical properties of the hyporheic zone are influenced by mixing of discharging groundwater and riverbed infiltration which will have a large impact on the subsurface biological patterns (Duff and Triska 2000). The physical, chemical and biological conditions of the hyporheic zone allow it to have a filtering effect on water from groundwater and surfacewater sources (Fig. 1:6). Physical filtration is the simplest mechanism where filtration occurs by physically blocking particles passing through the substrate for example, infiltration of coarse particulate organic matter (CPOM) will be attenuated as flow paths increase in length both vertically and horizontally. Biological filtration occurs when nutrients dissolved in either groundwater or surfacewater are taken up or transformed by microbial biofilms coating alluvial sediments. Chemical filtration involves precipitation and redox reactions, and will vary dependent on the local geological conditions (Harvey and Fuller 1998, Hancock et al. 2005, Gandy et al. 2007). The three filtration mechanisms can occur concurrently or consecutively.

Dissolved oxygen will decrease with increased residence time of water in the hyporheic and again this is affected by hydraulic conductivity. Similarly attenuation of CPOM (Crenshaw

et al. 2002, Navel et al. 2011a) and uptake of dissolved organic carbon (DOC) (Chestnut and McDowell 2000) will be influenced by sediment size and residence time of water in the hyporheic zone (Brunke and Gonser 1997). For example, in streams draining chalk and sandstone catchments fine pore spaces result in high capillary forces and subsequently slow through flow times with biogeochemical gradients possibly restricted to a few centimeters. Inputs of fine sediment to the hyporheic zone, particularly in areas of naturally occurring fine sediments can have a deleterious effect on hyporheic faunal assemblages decreasing both abundance and diversity (Quinn and Hickey 1994, Weigelhofer and Waringer 2003a). The problem of sediment input to streams from agriculture is a widespread problem, with attempts to reduce clogging bringing only temporary relief to the system unless the source of fine sediment is removed (Kasahara and Hill 2006). Burrowing by hypogean fauna in the hyporheic zone is an important functional process with bioturbation reducing clogging and increasing subsurface flowpaths (Nogaro et al. 2006). Bioturbation and grazing of bacteria by tubificids can stimulate bacterial processes which will contribute to the retention of organic matter in the hyporheic zone (Traunspurger et al. 1997, Mermillod-Blondin et al. 2004).

Streams and rivers draining for example, limestone or basalt catchments contain a sediment matrix of large pebbles and cobbles and subsequently sediments have a low capillary action and fast throughflow times. Fast throughflow times result in an increase in DO levels in the hyporheic zone with replenishment often exceeding uptake, thus benefitting both epigeal and hypogean fauna (Dole-Olivier et al. 1993, Malard and Hervant 1999). Coarse sediments tend to be well sorted with clearly defined pore spaces which epigeal and hypogean fauna can swim or crawl through with many elongate fauna proliferating (i.e. Plecoptera larvae and Elmidae larvae) (Ward and Voelz 1998).

Nutrients

In temperate streams with a well-developed riparian zone, the dominant source of organic matter will be from leaf litter entering the stream during autumnal leaf fall. Much of the carbon and nutrients contained in the leaf litter is subsequently buried within the sediments during flood events (Metzler and Smock 1990, Crenshaw et al. 2002, Navel et al. 2011b). Leaf litter breakdown rates in the hyporheic zone are considerably slower than rates in the benthic zone. Fungal and invertebrate processing rates are lower in the hyporheic zone, although the relative contribution of fungal processing rates to invertebrate processing rates can be proportionally higher (Cornut et al. 2010). Leaf litter buried within the hyporheic zone is broken down to fine particulate organic matter (FPOM) by shredders (Kelly et al. 2002, Navel et al. 2011b) and by mechanical processes occurring within the river bed sediments (Schlief and Mutz 2009). Bioturbators and physical forces further breakdown FPOM to dissolved organic matter (DOM) which is then available for uptake by bacteria leading to reduced or oxidized end products (Freckman et al. 1997). Studies have shown epigeal fauna, in particular *Gammarus* sp. to actively shred leaf litter in the shallow hyporheic sediments. The resulting FPOM is consumed by stygobite fauna such as *Niphargus* sp. in the hyporheic zone and deeper sediment layers (Crenshaw et al. 2002, Navel et al. 2011b).

Movement and retention time of water through subsurface sediments directly influences the uptake of dissolved and particulate organic substances with reduced and oxidised reactions dependent on hydraulic conductivity and DO (Rulik et al. 2000). The increase in allochthonous biomass through the uptake of DOM by bacteria is fed back into the stream by the grazing of microbial biofilms by hypogean fauna such as copepods (Pusch et al. 1998, Ward and Voelz 1998). Upwelling groundwater can also be rich in minerals and nutrients (Boulton and Foster 1998, Datry et al. 2007) with upwelling groundwater often supporting diverse and stable communities of epigeal and hypogean fauna (Malard et al. 2003a). The

increased residence time of water in the hyporheic zone and reduction of oxygen will also limit microbial respiration (Baker et al. 1999). When anoxic conditions develop in the hyporheic zone respiration requires alternative terminal electron acceptors with the utilisation of nitrate preferentially used.

Nitrate concentrations in many UK rivers and groundwaters have increased consistently during the last 30 years with increases commonly associated with agriculturally impacted catchments (Howden and Burt 2009). Nitrogen is one of the most important elements contained in living matter with approximately 10% of the dry mass of bacteria is nitrogen (Duff and Triska 2000). In streams and rivers with high nitrate levels there is considerable evidence that the hyporheic zone provides an important functional role in denitrification processes (Cooke and White 1987, Fischer et al. 2005). Denitrification rates are higher when sediment surface area is larger, also hydraulic conductivity will be lower resulting in a greater uptake of nitrates and associated DOC (Fischer et al. 2005). Denitrification processes in the hyporheic zone of a southern English chalk stream removed up to 31% of the riverine nitrate loads (Wexler et al. 2011). Denitrification in the hyporheic zone is complex and highly variable across systems with other studies reporting limited denitrification processes in English chalk streams, particularly when oxygen concentrations are sufficiently high (Pretty et al. 2006).

Oxygen

The amount of DO in subsurface sediments depends on the permeability and porosity of the substrate, saturation of the sediments and aerobic respiration. Sediments with low porosity and permeability will have low DO concentrations (i.e. alluvial sediments of flood plains) with species assemblages in these hyporheic habitats impoverished and dominated by Nematoda and Oligochaeta (Ward et al. 1998). In coarse sediments (i.e. mountain streams) DO concentrations can be high with species assemblages diverse and containing a large

proportion of epigean species (Ward et al. 1998). In deeper sediment layers of the hyporheic zone anoxia is common with oxygen replenishment slow (Holmes et al. 1994, Malard and Hervant 1999), in these environments groundwater and hypogean taxa are common being more tolerant of hypoxia than epigean species. For example, the hypogean amphipod *Niphargus* sp. could be kept for two months in water containing $0.5\text{mg l}^{-1}\text{ O}_2$, whereas the epigean amphipod *Gammarus* survived for only a few days (Danielopol 1989). Oxygen depletion in the hyporheic zone affects all aerobic fauna with a few capable of withstanding anoxic conditions for a limited time, such as some nematode species (*Tobrilus gracilis*) can tolerate anoxia well (Schiemer and Duncan 1974, Nold et al. 2010). This adaptation suits hypogean fauna to life in the hyporheic where DO concentrations can vary considerably.

Seasonality and flood events can also influence DO concentrations with increasing groundwater discharge into the hyporheic zone inducing spatial and temporal shifts in oxygen availability in the hyporheic zone (Soulsby et al. 2009). This seasonal shift is borne out in patterns of hyporheic fauna in up- and downwelling zones with epigean fauna associated with downwelling zones and hypogean fauna with upwelling zones (Dole-Olivier et al. 1997). Species richness is also affected at large spatial scales by up- and downwelling zones, for example gaining sections along an alluvial river in New Zealand had significantly higher species richness than losing sections, this was attributable to flow permanence (i.e. greater in gaining sections) along the river (Datry et al. 2007)

Disturbance

Disturbance is a major factor controlling many aspects of stream ecology such as metabolism, faunal dynamics and patchiness (Resh et al. 1988). Flooding is a major form of natural disturbance in streams and also one of the most important factors shaping the hyporheic zone (Olsen and Townsend 2005). The hyporheic zone can provide resilience to a river ecosystem providing refugia for surface invertebrates, for example during flood

episodes (Boulton and Stanley 1995, Brunke and Gonser 1997) and droughts (Holsinger and Dickson 1977, Wood et al. 2010). In a typical stream reach the hyporheic zone contains patches of coarse and fine sediments with communities arrayed through the various sediment layers (Brunke and Gonser 1997). This distribution is also dynamic and changeable, particularly following disturbance events such as floods. In a study on the Kye Burn, New Zealand, the proportion of fine sediments (<1 mm) in the hyporheic zone (10–50 cm) increased over three sampling occasions (before, 2 days after and 1 month after a flood). Median particle size of the sediment also declined although sediment porosity did not change (Olsen and Townsend 2005).

In a study on a gravel bar along the Rhone River in Lyon, France, the hyporheic zone acted as a patchy refugium with differences between up- and downwelling zones (Dole-Olivier et al. 1997, Dole-Olivier 1998). The downwelling site on the Rhone had the greatest amount of migration by epigeal fauna (*Gammarus* sp., Cladocera) and hypogean fauna (Cyclopoida, Harpacticoida) during flood episodes with vertical migration of stygobite taxa (*Niphargus* sp., *Niphargopsis*) also recorded (Dole-Olivier 1998). Movement within a substrate is only possible if the interstitial space allows it, therefore size and type of sediment is a major factor in the use of the substrate as a refuge. Vertical migration was less important in the upwelling sites on the Rhone River with lower species numbers and densities. Vertical migration has also been shown to be less important in sandy substrates. In a study in a stream in Northern Virginia, USA, Palmer et al (1992) found a significant loss of meiofauna from the streambed during two floods which varied in magnitude, in each flood between 50–90% of the fauna was lost from the bed during both flood events despite the fact that the depth of scour (10–30 cm) was significantly less than the total depth of the hyporheic zone (50 cm). This suggests the hyporheic zone may serve as a partial source of colonists following disturbances although movements down into sandy substrates were not sufficient to prevent significant losses of meiofauna during floods. In flume experiments

Palmer et al., (1992) detected small scale (m^{-2}) migrations into sediments for some taxa (Copepods, Chironomids) in response to increased water flow.

The hyporheic zone can also be a refuge from oscillations of temperature in surfacewater with temperature fluctuations in the hyporheic zone are attenuated with increasing depth. This dampening of temperature fluctuations with depth is also important for temperature dependent ecosystem processes i.e. invertebrate development and microbial activity (Brunke and Gonser 1997). In winter, the hyporheic zone is often warmer than surfacewater, whereas in summer it is often cooler with upwelling groundwater thermally distinct from adjacent waters (Malard et al. 2001, Burkholder et al. 2008). Importantly the hyporheic zone can act as a refuge for epigeal fauna from high temperature spikes in summer and low spikes in winter providing a stable thermal environment for hypogean fauna.

Hyporheic ecology

Our ecological knowledge of groundwater and hyporheic systems has lagged far behind that of lakes and rivers (Boulton et al. 2003a, Deharveng et al. 2009). During the last 25 years the inclusion of the vertical dimension in the majority of ecosystem conceptual models has become an explicit requirement (Thorpe et al. 2006). This incorporation has fuelled research into the hyporheic zone, in particular the contribution of the hyporheic zone to whole stream metabolism (Boulton et al. 2010). In the hyporheic zone, rates of metabolism are controlled by water flowing through the sediments, which is in turn controlled by the sediment composition governing the flow velocity of interstitial water flow (Findlay 1995). The contribution of the hyporheic zone to whole stream metabolism is well documented (Baker et al. 1999, Fellows et al. 2001, Fischer et al. 2005) with the contribution of the hyporheic zone to ecosystem respiration (R) increasing as groundwater-surfacewater connectivity increases (R ranging from 43% to 98%).

Interactions across ecosystem boundaries are well documented in ecology (Polis et al. 1997, Knight et al. 2005), and particularly important in temperate streams. For example, the input of autumnal leaf litter from riparian zones and export of aquatic insects during summer emergence (Richardson et al. 2009). The linkages between streams and the hyporheic zone are particularly important with inputs of DOC from groundwaters supporting the growth of biofilms in the hyporheic zone which then become available for higher trophic levels (Fiebig 1995). The hyporheic zone can also act as a storage zone for autochthonous and allochthonous organic matter, this is broken down to DOC and also taken up by biofilms and consumed by higher trophic levels (Battin et al. 2008).

Sediment composition is important in the hyporheic zone as it provides a medium for microbial growth, a supply of solutes from mineralisation processes and controls the rate of water flow through the sediments. Controlling water flow will also control connectivity between groundwater and surfacewater, hydraulic conductivity and the uptake of DO and nutrients. Therefore the main influences on hyporheic ecology are hydraulic conductivity, DO and nutrients (Sharp 1988). General patterns also occur in streams with a decrease in sediment size as stream order increases, coupled with an associated decrease in hydraulic conductivity (Heitmuller and Hudson 2009).

Hyporheic assemblages (hyporheos)

The hyporheic zone where groundwater and surfacewater interact is a unique environment containing biological and chemical characteristics of both surfacewater and groundwater and to succeed in this environment specific adaptations and life histories are required. The absence of the nycthemeron (i.e. the natural day and night) is the most obvious factor of the hypogean environment that makes it unique. The hyporheos often display highly specialised adaptations to cope with the absence of light enabling them to prosper in this unique environment. The classic responses of organisms to the absence of light are lack of skin pigmentation, ocular regression and hypertrophy of sensory organs. Appendages are

generally long and numerous and allied with highly developed chemical and mechanical receptors (Gibert and Deharveng 2002). Reduced metabolic rates are also common in subterranean fauna with food scarcity dictating a more efficient use of available resources (Wilhelm et al. 2006) for example; *Niphargus* sp. can store lipids for utilisation during periods of food scarcity (Dhomps-Avenas and Mathieu 1983). Temperature is an important variable in the hyporheic zone with temperature fluctuations attenuated with depth. This dampening of temperature fluctuations is important for temperature dependent ecosystem processes such as invertebrate development and microbial activity (Brunke and Gonser, 1997). In winter, the hyporheic zone is often warmer than surface waters, whereas in summer it is often cooler with upwelling groundwater thermally distinct from adjacent waters (Malard et al., 2001; Burkholder et al., 2008).

Hypogean fauna

The hyporheic zone is where surfacewater and groundwater mixes and therefore the hyporheos is also composed of both epigeal and hypogean taxa. There are numerous ways of classifying these taxa based on their varying reliance on sub-surface waters during their life cycle. The consensus of groundwater biologists is to adopt the classification proposed by Gibert et al., (1994) (Fig. 1:7). This is a functional classification based on the morphological and physiological adaptations that invertebrates possess to a subsurface existence, ranging from primarily surface dwelling fauna (stygoxene) to obligate groundwater invertebrates (stygobite):

Stygoxenes: These organisms have no affinities with groundwater systems but they may occur accidentally in alluvial sediments or caves and act as predators or prey of hypogean taxa (e.g. Simuliidae (Diptera), Heptageniidae (Ephemeroptera)).

Stygophiles: Show a greater affinity for groundwater appearing to actively exploit resources and/or use the hyporheic zone and groundwater as a refuge from surface events such as flooding or predation (e.g. *Caenis* sp. (Ephemeroptera), Plecoptera larvae).

Stygobites: Specialized subterranean forms such as the beetle *Hydroporus ferrugineus*. Some are ubiquitous in all types of groundwater systems (e.g. cave systems, alluvia, hyporheic) for example the amphipod *Niphargus aquilex*. However, some are phreatobites, restricted to the deep groundwaters (i.e. phreatic zone) of alluvial aquifers, for example *Niphargus kochianus* in the UK.

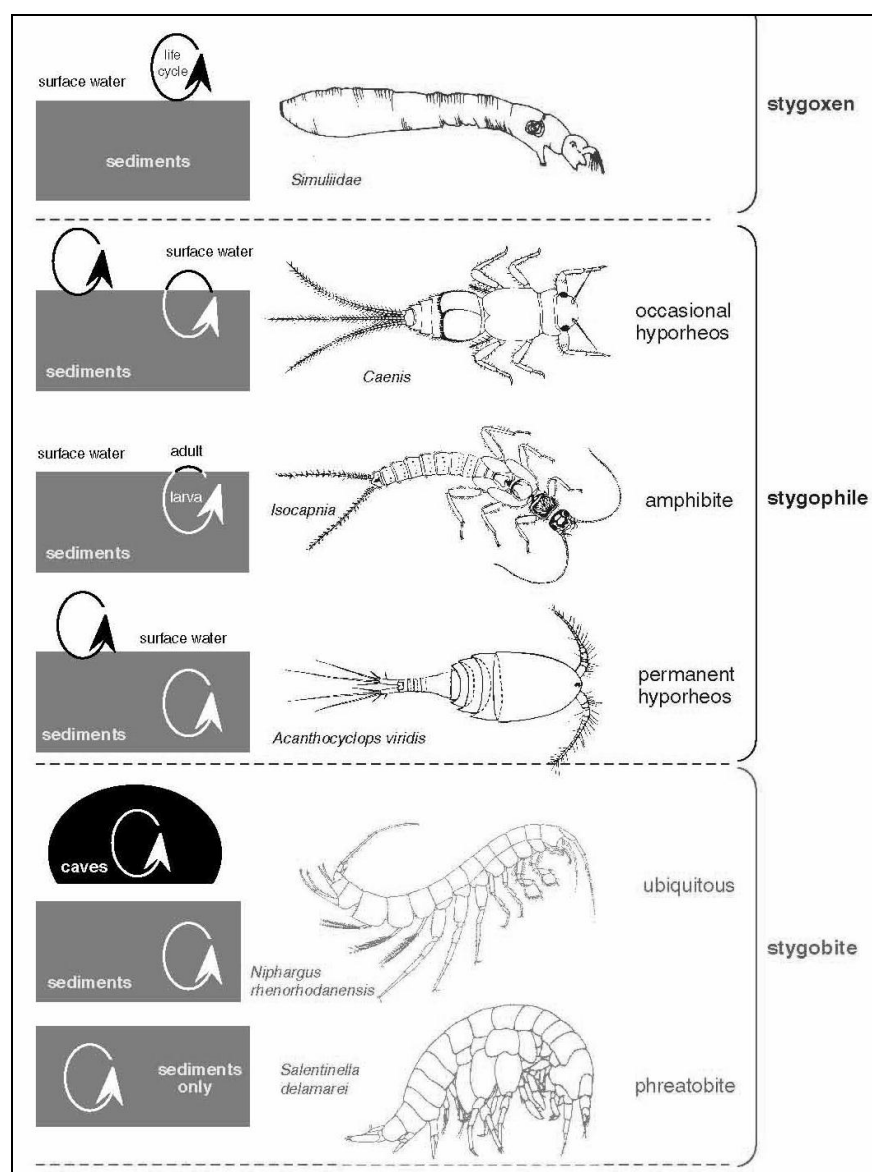


Figure 1:7. Classification of groundwater fauna describing their affinity for life in the hyporheic and groundwater habitats (Gibert et al. 1994).

Groundwater and alluvial sediments are a fundamental resource for organisms with hypogean environments containing diverse biological assemblages (Danielopol et al. 2003). In 1986 an extensive review of hypogean fauna of the world found 6634 known aquatic stygobites (Botosaneanu 1986) and by the year 2000 this number had risen to 7,700 (Gibert 2004). A recent European project (PASCALIS 2008) collected 100 new European aquatic stygobite species with this number continuing to rise as further geographic areas are explored (Ferreira et al. 2007, Deharveng et al. 2009). In some aquatic groups, in particular microcrustacea a high proportion of the total biodiversity is found in subterranean habitats (Rouch and Danielopol 1997, Sket 2004, Ferreira et al. 2007, Deharveng et al. 2009). In Europe the subterranean environment is unique compared to surface environments because it includes a large number of endemic and rare species for example, up to 78% of the stygobitic taxa in the Dinaric region are endemic to that region (Sket 2004). Biodiversity hotspots in groundwaters are often associated with karstic areas and coarse alluvial sediments where well oxygenated water and organic matter penetrates easily into the subsurface sediments (Dole-Olivier et al. 2009b, Galassi et al. 2009b). Within karstic habitats stygobite species can have a wide distribution, particularly in the saturated zone. In the unsaturated karstic areas groundwater habitats can become highly fragmented increasing vicariance events and leading to high levels of endemism and speciation (Galassi et al. 2009b).

Endemism and speciation require time to develop and levels of endemism decrease in northern latitudes affected by Quaternary glaciations (Stoch and Galassi 2010). In the UK at present only one endemic species has been recorded, the Amphipod *Niphargus glenniei*. Low numbers of recorded stygobite species in the UK are suggested to be a result of Quaternary glaciations although extensive surveys of subterranean habitats in the UK are few at present (Robertson et al. 2009). The influence of Quaternary glaciations has also been shown to affect endemism in continental Europe. In a study on the Walloon karst in

Belgium, an area also affected by Quaternary glaciations, endemism was low in comparison to similar sites further south in Europe with the stygobites collected likely to have re-colonised the Walloon area post glaciation (Martin et al. 2009).

Epigean fauna

The hyporheic zone, in particular the shallow hyporheic is often dominated by epigean fauna with dominance decreasing with increasing depth with hypogean fauna increasingly dominant (Brunke and Gonser 1999). In a study on the Toss River, Switzerland, Brunke and Gonser., (1999) found epigean fauna such as *Gammarus* sp. and *Leuctra* sp. common in the shallow hyporheic (20cm depth). At intermediate depths (30cm depth) copepods were abundant with hypogean taxa common in the deep hyporheic layers (50cm depth), this pattern has also been found in other similar studies (Davy-Bowker et al. 2006, Omesova et al. 2008, Marmonier et al. 2010). The number of species collected in the hyporheic zone varies considerably across geographical areas and geologies, with high species diversity common and often dominated by epigean meiofaunal species. In a study conducted on a sandy stream in Goose Creek, Northern Virginia by Turner and Palmer., (1996) over 145 species of meiofauna were found, while a study at the Oberer Seebach, a gravel stream in Austria, found over 300 species (Schmid-Araya 1997).

Table 1:4. Stygobites species currently recorded in England and Wales (Robertson et al. 2008).

Class	Order	Family	Genus/species
Crustacea	Amphipoda	Niphargidae	<i>Niphargus aquilex</i> (Schiodte, 1855)
			<i>Niphargus fontanus</i> (Bate, 1859)
	<i>Niphargus glenniei</i> (Spooner 1952)		
	<i>Niphargus kochianus kochianus</i> (Bate, 1859)		
	<i>Microniphargus leruthi</i> (Schellenberg, 1934)		
		Crangonyctidae	<i>Crangonyx subterraneus</i> (Bate, 1859)
	Isopoda	Asellidae	<i>Proasellus cavaticus</i> (Leydig, 1871)
	Syncarida	Bathynellidae	<i>Antrobathynella stammeri</i> (Jakobi, 1954)
	Copepoda	Cyclopoida	<i>Acanthocyclops sensitivus</i> (Graeter & Chappuis, 1914)
Insecta	Coleoptera	Dytiscidae	<i>Hydroporus ferrugineus</i> (Stephens 1829)

Hyporheic research in the UK

Hyporheic studies in the UK are rare, particularly in comparison to continental Europe (PASCALIS 2002, Dole-Olivier et al. 2009a), North America (Stanford and Gaufin 1974, Hunt and Stanley 2003) and Australia (Boulton and Foster 1998, Boulton et al. 2003b). The UK studies currently undertaken on the hyporheic zone have been concentrated in the south on chalk (Wood and Armitage 1997, Davy-Bowker et al. 2006, Wood et al. 2010) and sandstone (Rundle and Hildrew 1990, Stead et al. 2003, Stead et al. 2004) geologies. However, research on karst geologies in continental Europe has shown these areas to be biodiversity hotspots (Rouch and Danielopol 1997, Dole-Olivier et al. 2009b, Stoch and Galassi 2010), with karstic areas of the UK potentially rich in biodiversity. Research undertaken in the UK has shown pH to be a strong driver of microcrustacea abundance and distribution in the hyporheic zone, as it is in epigeic habitats (Rundle 1990, Rundle and Hildrew 1990). Larger scale studies in the UK have also been undertaken, with Rundle and Ramsay., (1997) describing lowland and upland communities of the hyporheos with pH again explaining a large proportion of differences between the two communities.

Recently a large project was undertaken in Scotland attempting to describe the distribution and composition of the hyporheos of Scottish streams which were all impacted by the Devensian glaciation (Pryce et al. 2010). This study collected no stygobite species further supporting the view that the last glaciation extirpated many stygobite species, with subsequent recolonisation also slow. Current stygobite species records for the UK are listed in Table 1:4 with few species collected in comparison to continental Europe, although one species (*Niphargus glenniei*) is endemic to the UK and a UK Biodiversity Action Plan candidate species and the water beetle *Hydroporus ferrugineus* is Red Data Book notable. There are relatively few records of stygobites in England and Wales and it is possible that further species yet await discovery.

In light of the paucity of hyporheic studies in the UK particularly on karst systems, this study will examine a range of UK hyporheic communities occurring across different hydrogeological regions. The geologies chosen for the study are porous and associated with aquifer types which provide a significant contribution to surfacewater stream flow and surfacewater–groundwater interactions are strong (hyporheic zone). The emphasis in this study will be the meiofaunal invertebrate community, in particular microcrustacea. Species richness and abundance of microcrustacea in subsurface sediments of continental Europe is high, particularly in areas unaffected by recent glacial events. Consequently, in this study the emphasis will be on geologies with a carbonate content reflecting the focus on microcrustacea. Study sites will be located hydrogeological regions with a specific sediment composition (i.e. sediment size) and subsequently a range of hydraulic conductivities within subsurface sediments. Study sites will be predominately located to the south of the southern extent of the Devensian glacial limit where biodiversity and species richness is unaffected by glacial events. To assess the effect of glaciation, sites on karst geologies will also be chosen to the north and south of the Devensian glacial limit.

The importance of the hyporheic zone as an ecotone between groundwater-surfacewater-riparian zones is accepted within ecology, with dynamic biological and chemical ecotones occurring between each zone supporting distinct communities of micro- meio- and macrofaunal communities. Hydrogeology, in particular the sediment characteristics of the hyporheic zone will influence the hyporheos through accessibility of the interstitial spaces and physico-chemistry parameters and consequently the ecotonal properties. This thesis examines the influence of sediment type on the physico-chemistry and the invertebrate assemblages in the shallow (20cm) and deep (50cm) hyporheic zones of the UK north and south of the Devensian glacial extent. The three hydrogeological areas chosen for the study exhibit a range of hydraulic conductivity properties from a stable flow regime (Cretaceous

Chalk), intermediate flow regime (Permo-Triassic Sandstone) to a highly variable flow regime (Carboniferous limestone).

Aims and objectives of the thesis

The preceding literature review has highlighted the importance of the hyporheic zone within stream ecology and the influence hydrogeology and recent glaciations can have on hyporheic assemblages. The primary aim of this thesis is to understand how hydrogeology and glacial legacy influences hyporheic invertebrate assemblages of the UK. To address this overarching aim the following broad hypotheses were tested using the methodology outlined in chapter 2:

- 1) In chapter 3, the role of hydrogeology on hyporheic physicochemistry will be addressed. I hypothesize that coarse sediments represented by the carboniferous limestone deposits will exhibit low concentrations of dissolved minerals, greater vertical hydraulic connectivity, high oxygen content and organic matter than finer sediments represented by chalk and sandstone geologies.
- 2) In chapter 4, species – environment relationships will be addressed with a focus on abundance, species richness, body size and stygobite distribution (post Devensian glaciation) with the following three broad hypotheses tested:
 - a) Stygobite fauna will be higher in abundance at sites south of the southern extent of the Devensian glacial limit compared to sites north of the limit.
 - b) Species richness and abundance of invertebrate fauna in the hyporheic zone will be highest in coarse sediments (i.e. limestone) with species richness and abundance lower in geologies containing more fine sediments (i.e. chalk, sandstone).
 - c) Large bodied invertebrate fauna will be more abundant in the hyporheic zone of coarse sediment (i.e. limestone) where interstitial space is greatest.

3) In chapter 5 the influence of sediment size on hyporheic assemblages will be addressed experimentally. This will be done at the reach scale rather than regionally with the following broad hypotheses tested:

- a) Physicochemical parameters will vary between sediment treatments with treatments containing a high proportion of coarse sediments characteristically high in dissolved oxygen, CPOM and low in dissolved minerals, with reverse patterns evident as the proportion of fine sediment increases.
- b) Species richness and abundance of invertebrate fauna in the hyporheic zone will be highest in coarse sediments with abundance reducing as the proportion of fine sediment increases.
- c) Body size of invertebrate fauna will be smaller as sediment size reduces and interstitial space also reduces.

The preceding hypotheses will be developed further in the relevant individual chapters using field surveys and experimental methods.

Chapter II: Methodology

Introduction

A major reason for the paucity of studies on the hyporheic zone in the earlier years of river research is the inaccessibility of the environment (Hunt and Stanley 2000, Scarsbrook and Halliday 2002). Hyporheic sampling methods developed to overcome the problem of inaccessibility are numerous, with extensive reviews of the pros and cons of each method (Bretschko and Klemens 1986, Hunt and Stanley 2000, Scarsbrook and Halliday 2002, Boulton et al. 2003a, Kibichii et al. 2009). Sampling of the hyporheic zone will either involve the removal of sediments, interstitial water and fauna using a coring device or extraction of interstitial water and fauna using a pump or bailer.

Coring techniques extract nonfrozen or frozen sediment cores, with the removal of nonfrozen cores involves the insertion of a corer into the sediments, the corer is then twisted which allows a chamber within the corer to fill with sediments (Williams 1989). The corer device works well in soft sediments though penetration and removal of coarse sediment can be problematic. Freeze coring methods involve the insertion of the corer into the sediments along with two insulated copper rods (Olsen and Townsend 2003). The rods are used to emit an electrical field to immobilise fauna and prevent migration away when the liquid nitrogen is inserted. Freeze coring is the best quantitative method available for sampling the hyporheic zone, though the logistics involved when multiple sites are to be sampled make the method ill-suited to large scale field campaigns.

Pumps and bailers involve the insertion of a piezometer into the stream bed which can be driven down to a specific depth. Then a pump device is attached to the piezometer and a specific volume of water removed. The pump sampler is a semi-quantitative method due to water drawn into the piezometer is extracted from the surrounding area which is difficult to

define accurately. Pump devices commonly used include the BOU-ROUCHE pump and hand bailers.

Alternative methods for sampling the hyporheos include Karaman-Chappuis method and colonisation traps. The Karaman-Chappuis method (Karaman 1935) involves digging a hole in exposed riverbed sediments to below the water table. The hole then fills with water from the exposed sediments allowing a sample to be collected once the hole is filled with water. This method is simple and effective when exposed sediments are available. The limitations are that initially exposed sediments (e.g. parafluvial zones, islands) are required with sampling limited to the shallow hyporheic zone. Colonisation traps fall into two categories: (1) standpipe traps where access into the sediments is by a pre-inserted tube (James et al. 2008) and (2) colonisation traps that are inserted into pre-excavated holes, then reburied until removal is required and then excavated (Scarsbrook and Halliday 2002).

All methods require the disturbance of sediments through insertion of a corer, piezometer or excavation with all methods requiring the initial disturbance of hyporheic sediments. Settling periods (1 - 2 hours) should be used following disturbance of sediments to allow recolonisation of fauna. In this study the use of freeze coring is not logistically possible due to the number of sites sampled. The non-frozen corer could be a useful tool if sediments are fairly soft (e.g. chalk and sandstone) although limestone sediments would make this method difficult to use. Colonisation traps were not used for the main field study as a sample from the natural sediments present in the hyporheic was required. The pump sampler is the method chosen for the field study being relatively simple to operate and while losing precision vertically, the numbers of samples that can be taken with the method enable a more accurate assessment of the hyporheos. The experimental study will use colonisation traps allowing sediment types to be inserted into the hyporheic in a controlled manner.

Table 2:1 Location of study sites selected for the investigation of hydrogeological influences on hyporheic assemblages. Four riffles were chosen from each catchment and the head and tail of the riffle sampled. Sampling was undertaken in the summer and winter of 2008. During the summer, samples were taken from both the head and tail of the riffle with 3 replicate samples taken at 20cm and 50cm depth (n = 384). During the winter samples were taken from the head and tail of the riffle with three replicate samples taken from 50cm depth only (n = 192). Elevation accuracy was +/- 5 metres.

Geology, county and river catchment	Location	River	OS grid reference	Elevation (metres)
Cretaceous Chalk				
Dorset - Frome catchment	Chilfrome	Frome	SY59079912	95
	Godmanstone	Cerne	SY66949794	79
	Grimstone	Sydling Water	SY63879490	78
	Maiden Newton	Hooke	SY59409762	89
Dorset - Piddle catchment	Briantspuddle	Piddle	SY81509338	44
	Athelhampton	Piddle	SY77359402	52
	Bere Regis	Bere Stream	SY84029528	45
	Waterston	Piddle		60
	Springs		SY74459513	
Permo-Triassic Sandstone				
Somerset - Tone catchment	Tyler Bridge	Halse Water	ST12502898	62
	Milverton	Hillifarance Brook	ST10922710	16
	Greenham	Tone	ST07852015	82
	Runnington	Tone	ST11852155	43
Devon - Exe catchment	Little Gornhay	Lowman	SS97701369	83
	Lower Creedy	Creedy	SS83950240	35
	Salmonhutch	Yeo	SX82759886	45
	Salmonhutch	Yeo	SX82859893	43
Carboniferous Limestone – glaciated during Devensian period				
Yorkshire Dales - Ure catchment	Marsett	Raydale	SD91108610	258
	Aysgarth	Bishopdale Beck	SE01538782	142
	Aysgarth	Walden Beck	SE01858780	126
	Arkleside	River Cover	SE04408075	85
Yorkshire Dales - Wharfe catchment	Buckden	Wharfe	SD93957740	211
	Buckden	Wharfe	SD93857720	209
	Arncliffe	Skirfare	SD92437242	231
	Arncliffe	Cowside Beck	SD92817150	225
Carboniferous Limestone – unglaciated during Devensian period				
Peak District - Derwent catchment	Castleton	Peakshole Water	SK15528320	166
	Buxton	Wye	SK09687250	255
	Monsal Dale	Wye	SK17057089	130
	Monsal Dale	Wye	SK17097134	128
Peak District - Dove catchment	Milldale	Dove	SK14095397	171
	Ilam	Manifold	SK13405065	138
	Dovedale	Dove	SK15005120	138
	Hamps Spring	Manifold	SK12765094	153

The last 25 years has seen a great increase in research in the hyporheic zone (Robertson and Wood 2010) and this has prompted the research community to standardise research methods

to allow comparability between datasets. In Europe the PASCALIS project (PASCALIS 2002) has undertaken a Europe wide study using standardised sampling methods. Groundwater and hyporheic biodiversity was described regionally with the BOU-ROUCHE pump used to extract hyporheic samples. This technique was also used in a smaller project studying the hyporheic fauna of Scottish gravel bed rivers (Pryce et al. 2010). Similarly, UK studies on the Ashdown Forest also used the BOU-ROUCHE method (Rundle 1990).

Sample volumes varied between the studies with 5 litres used in the PASCALIS and Ashdown Forest projects and 10 litres in the Scottish project. In a study by Boulton, et al. (2003a) optimal sample volumes were tested from 1 litre to 10 litres the 5 litre sample contained between 76-100% of the taxa collected in the 10 litre sample. Comparability of results and robustness of methods are important factors which should be considered when planning field studies. In this study we have attempted as much as possible for the results to be comparable with other concurrent studies and in particular the work undertaken by the PASCALIS project.

Study sites

Initial criteria for selection of the different geologies used in this study were hydraulic conductivity measures of the associated geological materials (Table 1.3). Increases in hydraulic conductivity are associated with a decrease in capillary action or increased grain size (Hiscock 2007). After selection of suitable geologies for the study, suitable field sites were then chosen using the following criteria derived from chemical and biological General Quality Assessment (GQA) scores (Table 2.2 & 2.3) provided by the Environment Agency: 1) chemical water quality parameters: between low (A) to moderate (C) and 2) biological quality parameters: between very good (A) to fairly good (C). Field sites were chosen on 3rd to 4th order streams with stream order derived from Ordnance Survey maps of the local area (Strahler 1964). The location of the field sites are given in Table 2:1 and Figure 1.3. One aspect of streams in karst systems is the difficulty defining catchment boundaries and stream

order precisely, therefore local knowledge of karst systems was utilised to identify the stream order as accurately as possible (Waltham et al. 1997). Riffles were chosen on the basis of good water flow with a minimum depth of 5cm. Bankwidths were similar across study areas ranging from 3-5 metres in width.

Carboniferous limestone

The Carboniferous rocks include Carboniferous Limestone, Millstone Grit and Coal Measures and can be broadly equated with the chronostratigraphical divisions Dinantian, Namurian and Westphalian. It was during the Dinantian that carbonate deposition was dominant represented by the Carboniferous Limestone and formed during a period of active tectonic movements. Dinantian rocks underlie study areas of the Yorkshire Dales and the Peak District and crop out in the areas shown in Figure 2:1 (Aitkenhead et al., 2002). The two carboniferous limestone areas have similar geologies and land use with the main difference between the two areas the impact of the Devensian glaciation. During this period the Yorkshire Dales were ice covered, whereas the Peak District was affected only by periglacial conditions making the two sites suitable for a comparative study on the effect of glaciation on the hyporheic zone.

Table 2:2. Environment Agency General Quality Assessment (GQA) chemical scores for nitrate.

Classification for nitrate grade	Grade limit NO ₃ (ppm) Average	Description
1	<5	Very low
2	>5 to 10	Low
3	>10 to 20	Moderately low
4	>20 to 30	Moderate
5	>30 to 40	High
6	>40	Very high

Table 2:3. Environment Agency biological assessment table using environmental quality indices (EQI) and average score per taxon (ASPT) indicating the environmental quality of a site.

Grade	EQI for ASPT	EQI for number of taxa	Environmental quality
A	1	0.85	Very good
B	0.99	0.7	Good
C	0.77	0.55	Fairly good
D	0.65	0.45	Fair
E	0.50	0.30	Poor
F	-	-	Bad

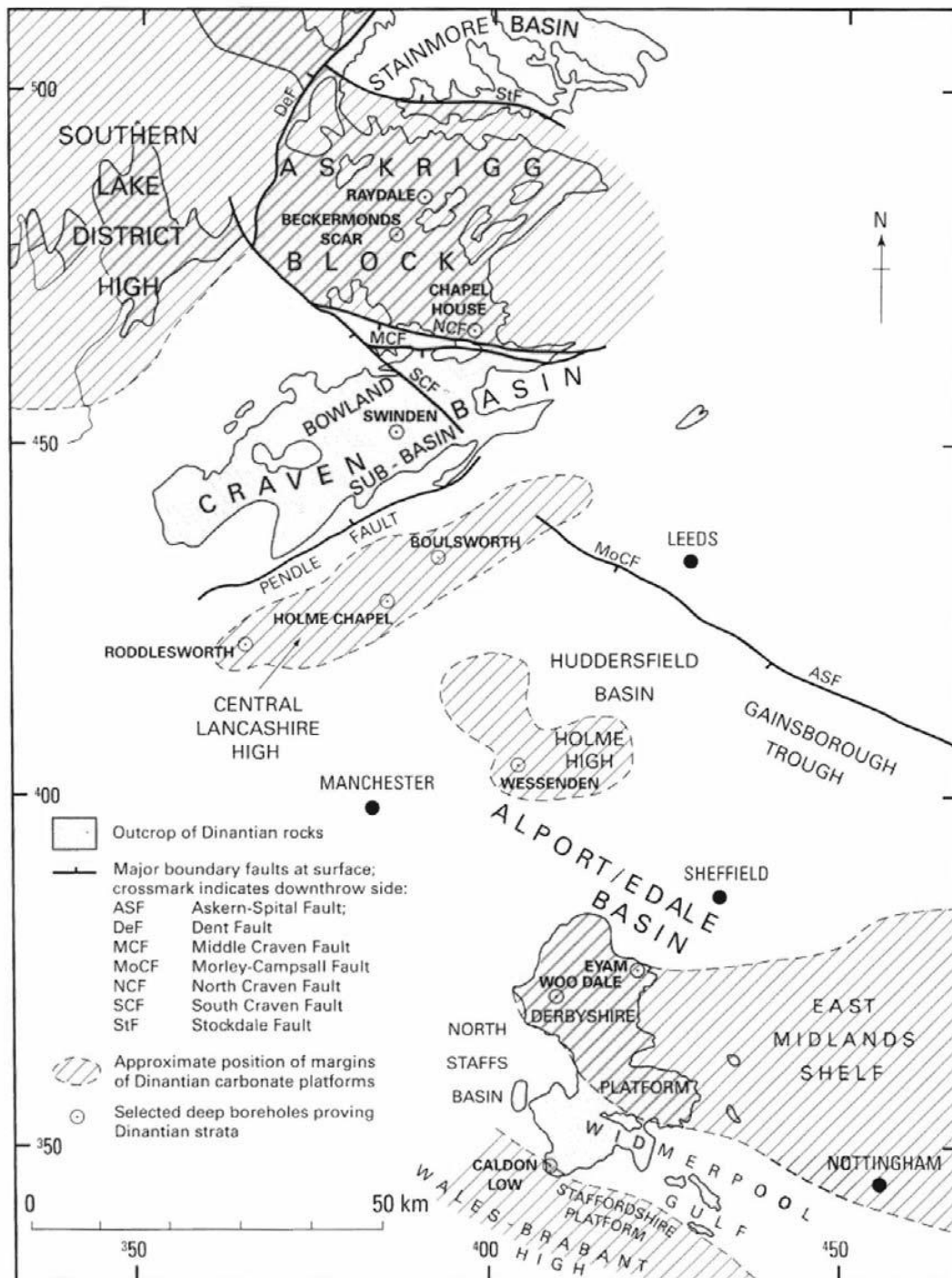


Figure 2:1. Outcrops of Dinantian carboniferous limestone deposits and principal structural features of the palaeogeography of the Peak District (Derbyshire Platform) and Yorkshire Dales (Askrigg Block) highlighting the similar geology of the two areas (Aitkenhead et al. 2002).

Yorkshire dales– glaciated

The two glaciated catchments chosen for the study are the Ure and Wharfe. The catchments lie within the Yorkshire Dales National Park and contain the best examples of glaciokarst in the UK (Howard 1998). During the Quaternary the area was glaciated on several occasions

with extensive glacial till deposits laid down over large parts of the area (Raistrick 1931, Evans et al. 2005). The thickness of the till varies greatly across the study area, with most deposits generally less than 4 m with thicknesses of up to 34.5 m also recorded. The two dominant limestone strata in the area are the Great Scar Limestone, a pure limestone about 180m thick and the Yoredale sequence which overlies the Great Scar limestone (Waltham et al. 1997). Yoredale is composed of a series of 4 or 5 thin bands of limestone intermixed with thin shales and occasional sandstones and exposed along valley sides (Waltham et al. 1997). Both types of rock exert characteristic influences over the landscape with Great Scar limestone a lighter coloured almost white rock outcropping to form dramatic cliffs (e.g. Kilnsey Crag near Malham). The Yoredales are slightly darker in appearance and exert the greatest influence outcropping for miles along the river valleys used in this study (i.e. Upper Wharfedale (Wharfe), Littondale (Wharfe), Langstrothdale (Ure) and Wensleydale (Ure)).

Ure catchment

The catchment area is 220 km² rising to over 600 m at its highest point. Mean annual rainfall is of the order of 1500mm yr⁻¹. The surface water quality at all sites in the Ure catchment is very good (Environment Agency, General Quality Assessment: chemical grade A (Table 2:2); bio grade A (Table 2:3)). Alluvial material in the Ure catchment is coarse grained and mean hydraulic conductivity measured at the site (pump time per litre) is high (17.7 secs/L⁻¹). Since deglaciation, the rivers have incised into the glacial deposits giving rise to a series of fluvial landforms, river terraces and alluvial fans (Howard et al. 2000). At higher elevations, gentle slopes and summits are covered by blanket peat which is extensively eroded, often to the underlying bedrock. Over 90% of the catchment is grazed or used for hay and silage, less than 5% is woodland which is mainly Sitka Spruce (Barlow 1998). Agriculture at all study sites is predominately hill farming with sheep farming on the upper slopes on unimproved pasture and cattle in the valley bottom on improved pasture.

Raydale is a short valley containing one of only two natural glacial lakes (Semer Water) in the Yorkshire Dales and located in the upper Wensleydale valley. The study site is located above Semer Water in the valley bottom where extensive meanders occur providing numerous riffle-pool sequences. The Raydale valley bottom is covered by alluvium of mixed fluvial and lacustrine origin overlying Great Scar limestone and with valley sides formed by rocks of the Yoredale series (Chiverrell et al. 2008). The catchment area is 43.6 km² rising to over 600m at its highest point. A detailed description of the Raydale valley is given in Chiverrell et al., (2008).

Two study sites are located in Bishopdale, one site on Bishopdale Beck and one site on Walden Beck. Bishopdale is a long, fairly narrow and deep low-lying u-shaped tributary valley of Lower Wensleydale with a geological profile similar to Raydale (Raistrick 1926). The second study site is located on Walden beck, a tributary of Bishopdale Beck. The geology of Walden beck is similar to both Raydale and Bishopdale with the lower section of Walden beck where the study site is located running along the Bishopdale valley.

Coverdale valley runs parallel to Bishopdale with a similar geology to both Raydale and Bishopdale with a detailed description given in Wilson., (1960). The River Cover runs north-east along the length of Coverdale entering the River Ure at Aysgarth. Similar to the other rivers in the Ure catchment the River Cover has extensive meanders and numerous riffle-pool sequences. The valley floor is broad and flat with extensive glacial till deposits which the river cuts through, the valley side's rise steeply from the valley floor with extensive scree slopes.

Wharfe catchment

The surface water quality of all sites in both the Wharfe and Skirfare catchment is very good (Environment Agency, General Quality Assessment: chemical grade A (Table 2:2); bio grade A (Table 2:3)). Mean annual rainfall is of the order of 1500mm yr⁻¹ in the catchments.

Alluvial material in the catchment is coarse grained and mean hydraulic conductivity measured at the site (pump time per litre) high ($18.52 \text{ secs/L}^{-1}$). The Wharfe catchment above Addingham covers an area of 427 km^2 and rises on the eastern flank of Pen-y-Ghent in the Northern Pennines at an altitude of 694m. Agriculture at all study sites is predominately hill farming with sheep farming on the upper slopes on unimproved pasture and cattle in the valley bottom on improved pasture.

The two study sites on the River Wharfe are located above and below the village of Buckden in the Upper Wharfedale valley. The valley is generally steep sided with a flat u-shaped valley floor with extensive meanders and numerous riffle-pool features. The geology of Wharfedale comprises layers of rocks exposed to the effects of glaciation. A detailed description of the upper Wharfedale valley is given in Raven et al. (2009).

The two study sites are located in the Littondale valley which contains the River Skirfare, tributary of the main River Wharfe; the study sites are located on Cowside Beck and the River Skirfare above Arncliffe. The study site located on the River Skirfare is perennial and fed by numerous springs entering the main river channel 400m above the highest upstream sample site. Above the springs, the river becomes ephemeral only flowing above ground during heavy rainfall. The Skirfare valley was glaciated during the Devensian period and exhibits a wide U-shaped valley with many karstic features including peripheral springs located at hydrological lows, also many littoral and submarine springs that emerge during hydrological highs. The Skirfare flows over a mixture of limestone pavement and alluvial deposits in the upper Littondale valley, alluvial deposits then dominate as the river enters its perennial stage at the sites chosen for this study (Abesser et al. 2005).

Cowside Beck is a tributary of the River Skirfare with a catchment of 20 km^2 and rises at an altitude of 400m and is seasonally dry in the upper reaches and predominately fed by springs. A number of tributaries enter Cowside Beck at 350m altitude where the stream becomes

perennial, Darnbrook Beck being the most important water supply to Cowside Beck (Gilbert et al. 2005). There are a number of seepages and springs along Lower Cowside Beck at the location of the study site, providing extensive subterranean flow to this section. A detailed description of the Skirfare and Cowside beck valleys is given in Gilbert et al., (2005).

Carboniferous limestone – unglaciated

The sites all lie within the Peak District National Park in the area known as White Peak located in north central England. During the Devensian glaciation the Peak District remained ice free with periglacial conditions dominating the area (Chiverrell and Thomas 2010). During glacial retreat at the end of the Devensian vast quantities of melting water from the glaciated areas to the north flowed south through the Peak District (Burek 1991). Meltwater carried large volumes of rock debris which cut through the layers of limestone producing the steep and craggy gorges which are a feature of the White Peak area (Burek 1991). The White peak is underlain by a broad anticline of carboniferous limestone covering an area 540km² (Gunn et al. 1998). The climate of the region is temperate with an annual rainfall of 1400mm y⁻¹. Agriculture at all study sites is principally low-intensity pastoral agriculture forming the heather and grass moorland on the valley sides and tops, with meadows and improved pastures in the lower valley floors.

Dove catchment

The surface water quality is good (Environment Agency, General Quality Assessment: chemical grade B (Table 2:2); bio grade B (Table 2:3)). Mean annual rainfall is of the order of 1500mmyr⁻¹. Alluvial material in the catchment is coarse grained and mean hydraulic conductivity measured at the study site (pump time per litre) is high (16.2 secs/L⁻¹). The River Dove rises on the Eastern side of Axe Edge and flows southwards. The River initially flows through Gritstone moorland characterised by extensive peat deposits and acidic soils. The river then flows through limestone country at Hollinsclough a section of the River Dove

immortalised by Isaak Walton (1653) in his book “The Compleat angler”. The river gains flow along its length despite an absence of tributaries due to numerous springs which occur along the length of the river (Wood et al. 2005). The upper limestone section of the Dove has a series of small stepped weirs which are a relic of Victorian river management. As the river enters Dovedale the weirs stop and numerous riffle-pool sequences are present.

The River Manifold rises at Flash Head on a similar moorland plateau to Axe Edge less than a kilometre south from where the River Dove rises. The river meanders through Gritstone countryside before reaching the limestone area at Ecton where the Manifold enters a deep limestone gorge. The Manifold is ephemeral losing substantial flow along its length (Wood et al. 2005) with the main river flowing underground from Wetton Mill to Ilam before emerging at Hamps Spring. The two study sites on the Manifold are located at the village of Ilam and at Hamps spring.

Derwent catchment

The rivers Wye and Derwent have similar surface water quality (Environment Agency, General Quality Assessment: chemical grade B (Table 2:1); bio grade B (Table 2:2)). Mean annual rainfall is of the order of $1500\text{mm}\text{yr}^{-1}$. Alluvial material in the catchment is coarse grained and mean hydraulic conductivity measured at the study sites (pump time per litre) is high ($15.1\text{ secs}/\text{L}^{-1}$). Peakshole water emerges from Peak Cavern located in the village of Castleton, and is on the boundary between the Dark Peak and the White Peak areas (Gunn et al. 2000). The ridge to the north of Castleton marks the beginning of the Gritstone and shale beds of the Dark Peak rising to the high moorland plateaux.

The River Wye begins at Wye head with a large catchment area (107 km^2) and numerous perennial and intermittent springs along the river length (Smith and Wood 2002). The river flows in a south easterly direction through Buxton and Bakewell to join the Derwent at Rowsley, 15 miles downstream. Below Buxton the River Wye runs through a series of deep

and narrow gorges where the first study site is located. The Wye then enters Monsal Dale where the valley widens out, though it remains steep sided at the locations of the two final Wye sites.

Cretaceous Chalk

The Dorset Chalk area lies at the western end of the Wessex Basin and is centred on the town of Dorchester. Cretaceous Chalk deposits are the dominant geological feature of both the Frome and Piddle catchments. The mean annual precipitation for the area is approximately 1025mm y⁻¹. Groundwater contributes a high proportion of the river flow, resulting in the stable flow regimes that are characteristic of chalk streams (Sear et al. 1999). Chalk underlies around 65 % of the catchment, sand and sandstone around 18% and argillaceous rocks such as clays and shales 11%. Drift deposits cover about 268.2 km² (41%) of the catchment which include clay-with-flints, alluvium and river terrace deposits (Edmunds et al. 2002). The general structural dip of strata within the catchment is to the east-south-east and the depth of present day erosion increases toward the west-north-west. As a consequence, the surface geology of the Frome/Piddle catchment comprises three distinct geological zones. These zones include Jurassic limestones and mudstones in the headwaters of the Frome and Piddle, chalklands in the middle reaches of the Frome and Piddle, with the lower reaches traversing the Palaeogene deposits of the Wareham Basin before the rivers discharge into Poole Harbour (Newell et al. 2002). A detailed description of the Frome and Piddle catchments is given in Edmunds et al. (2002). Land use in both catchments is predominately agricultural, comprising managed grassland with smaller areas of arable farming and forestry (Edmunds et al. 2002).

Piddle catchment

The Piddle catchment covers an area of 183 km² and ranges in altitude from 250 m on its northern divide to 50 m at the catchment outlet where it enters the River Frome. The surface

water quality is good (Environment Agency, General Quality Assessment: chemical grade C (Table 2:2); bio grade A (Table 2:3)). Alluvial material in the catchment is fine grained and mean hydraulic conductivity measured at the site (pump time per litre) is low (32.99 secs/L⁻¹). The Piddle and Bere Stream have few meanders with substantial realignment of the rivers since the 17th century through the development of water meadows and cress beds (Bettey 1977). As a consequence riffle-pool sequences are scarce on the rivers with site choice limited in comparison to the limestone and sandstone areas. We avoided areas of macrophytes during the summer campaign due to extensive areas of fine silts collecting in the macrophyte beds which would influence vertical connectivity.

Frome catchment

The River Frome catchment covers an area of 437 km² extending from Evershot on the Dorset/Somerset border to Poole Harbour (Casey and Newton 1973). The surface water quality is good (Environment Agency, General Quality Assessment: chemical grade C (Table 2:2); bio grade A (Table 2:3)). Alluvial material in the catchment is fine grained and mean hydraulic conductivity measured at the study sites (pump time per litre) is low (36.69 secs/L⁻¹). Below the source at Evershot the Frome is joined by the River Hooke at Maiden Newton. The study sites are located on the upper and middle reaches of the River Frome above the town of Dorchester, the only significant urban development along the study area. The two study sites located on the River Frome and River Hooke are located on similar geological deposits of Upper Greensand and Chalk (Casey and Newton 1973). The two study sites located on the River Cerne and Sydling Water are on pure chalk deposits (Casey and Newton 1973).

Permo-Triassic Sandstone

Permo-Triassic sandstone deposits are continental deposits from the great landmass of Pangaea dating from 295-250 million years ago for the Permian, and from about 250-203

million years ago for the Triassic. In general they represent continental, desert and semi-desert conditions. There are aeolian (wind transported) deposits, fluvial sediments and evaporites, including gypsum and halite (Kimblin 1995). Mean annual precipitation and runoff in the Tone upper catchment is approximately 1200 mm/yr⁻¹. The headwaters of the Exe and Creedy on Exmoor have a mean annual precipitation of 1700 mm/yr⁻¹.

Tone catchment

The Tone catchment covers an area of about 414km² and has its source in the Brendon Hills to the east of Exmoor. From its source to the confluence with the River Parrett at Bridgewater the Tone is 33km long and falls 370m (Nadolski 2004). The surface water quality is good (Environment Agency, General Quality Assessment: chemical grade C (Table 2:2); bio grade A (Table 2:3). Alluvial material in the catchment is fine-medium grained and mean hydraulic conductivity measured at the study sites (pump time per litre) is high (18.41 secs/L⁻¹). The geology along the River Tone catchment changes as you move from the headwaters to the confluence with the River Parrett. The Upper Tone valley above Greenham contains the oldest geology in the catchment, which is composed of faulted slates and shales, and classed as Minor Aquifer units (Gallois 2006). Further down the Tone valley at Greenham, Permo-Triassic sandstone and pebble beds dominate and form the major aquifers (Nadolski 2004). At all sites in the Tone catchment extensive meanders occur with numerous riffle-pool sequences present. The catchment is predominately agricultural with a mixture of arable and cattle grazing. In the upper reaches of the catchment farming is mainly permanent pasture with woodland common along the river banks. Below Greenham, farming becomes more intensive with a higher occurrence of arable farming and irrigation, woodland is still a common feature along the middle reaches of the river (Nadolski 2004).

Exe catchment

The Exe catchment covers an area of 1453 km² and has its source on the extensive moorland of Exmoor. The surface water quality is good (Environment Agency, General Quality Assessment: chemical grade C (Table 2:2); bio grade A (Table 2:3)). Alluvial material in the catchment is coarse grained and mean hydraulic conductivity measured at the study sites (pump time per litre) is high (19.26secs/L⁻¹). The Yeo and Creedy river catchments are underlain by rocks of Upper Carboniferous age in the Upper and lower reaches of the sub-catchment and by a variety of Permian rocks in the middle reaches (Harlow et al. 2006). The River Creedy and the River Yeo are large tributaries of the Exe draining a predominantly pastureland area, of relatively low relief, with extensive areas of woodland along the river valleys. The rivers Yeo and Creedy have extensive meanders and numerous riffle pool sequences.

The River Lowman has a wide floodplain containing abandoned channels and meander cut-offs, with numerous riffle-pool sequences. The catchment has substantial areas of woodland along the river banks, with farming in the catchment predominately pastureland (Lee 2005). The geology is similar to that found in the Yeo and Creedy catchments. All the study sites are located above major towns with only scattered small settlements occurring in the catchments.

Methodology

Survey design

Two rivers were chosen from each hydrogeological area: Cretaceous Chalk x 2; Permo-Triassic sandstone x 2; Carboniferous limestone (glaciated) x 2 and Carboniferous limestone (unglaciated) x 2, giving a total of eight river catchments selected for the study (Frome, Piddle, Exe, Tone, Ure, Wharfe, Dove and Derwent). At each river catchment four riffles were selected on both the main river and tributaries to maximise spatial coverage within the

each river catchment. Each sample site (riffle) was visited on two occasions 1) during low groundwater levels (summer) and 2) during high groundwater levels (winter). Sampling took place during June/July 2008 (summer) and October/November 2008 (winter). The sampling dates were chosen using groundwater level data available through the Natural Environment Research Council database (NERC 2011). The NERC database gives mean monthly levels and long term averages of groundwater for at least the last 20 years with data available with a time lag of two months for all major and minor aquifers in the UK. All sample sites on the selected rivers had permanent surface and hyporheic flow during the study period. During the summer, three replicate samples were taken at 20cm depth and three replicate samples at 50cm depth from both the head and tail of each riffle ($n = 384$). During the winter three replicate samples were taken from 50cm depth from both the head and tail of each riffle ($n = 192$).

The sampling design for both the summer and winter hyporheic sampling surveys and also the summer and winter glaciation effect surveys are outlined below:

Summer sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 2 depths = 384 samples.

Winter sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 1 depth = 192 samples.

Summer glacial effect survey: 4 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 2 depths = 192 samples

Winter glacial effect survey: 4 catchments x 4 riffles x (3 upwelling + 3 downwelling) = 96 samples.



Figure 2:2. Example of piezometer distribution across a riffle head. Piezometers are set laterally across the riffle head and located at least 1 metre apart and more than 2 metres from the river bank. The BOU-ROUCHE pump is attached to the piezometer on the left. A similar distribution of minipiezometers was used to measure vertical hydraulic gradients. Water chemistry was taken using probes inserted directly into each piezometer.

Hyporheic sampling method

The sampling method chosen was the BOU-ROUCHE method (Bou and Rouch 1967, Bou 1974). The BOU-ROUCHE pump has a high discharge rate (up to 0.66 L s^{-1}) and dislodges the majority of hyporheic fauna and sediment located in the vicinity of the piezometer tip (Bou 1974). The piezometer (2.5 cm internal diameter with 0.5 cm holes at the tip) was hammered into the riverbed using a sledgehammer to the required depth (20cm and 50cm). The piezometers were inserted laterally at the head and tail of each riffle and at a distance of at least 1 metre from the next piezometer and always more than 2 metres from the river bank (Fig. 2:2). The tail of the riffle was sampled first followed by the head of the riffle to minimise disturbance. The piezometers were then allowed to settle for at least 1 hour before

sampling was undertaken allowing fauna disturbed during insertion of the piezometer to recolonise.

After one hour the BOU-ROUCHE pump was attached to the piezometer then a volume of 5 litres of water extracted and pumped straight into a bucket. The volume of 5 litres was chosen after consulting literature describing the BOU-ROUCHE optimum sampling volumes (Boulton et al. 2003a, Kibichii et al. 2009). The pump requires priming (0.5 litre of filtered water (63µm mesh size)) before a sufficient draw is attained to enable a consistent flow through the piezometer and pump. The collected sample was then filtered through a 63µm mesh sieve, then rinsed and preserved in 70% industrial methylated spirits. The 63µm mesh size was selected so results could be easily compared to the PASCALIS project (Malard 2002).

Identification of meiofauna and macrofauna

In the laboratory samples were rinsed over a 63 µm sieve to remove fine silts from the sample. The cleaned sample was then poured into a tray and then elutriated three times to remove the lighter organic material. The sample collected in the sieve was then poured into a volumetric, agitated and then a 20% sub-sample withdrawn. In order to investigate whether any loss of explanatory power occurred with sub-sampling, five randomly selected samples were sub-sampled and processed. The 20% sub-sample and the remaining 80% of the sample were processed to estimate the sub-sampling efficiency (Table 2:4).

Sub-sampling accuracy was determined using the following formula:

$$\% \text{ accuracy of subsample (x)} = (\text{subsample total abundance} / \text{actual sample abundance}) \times 100$$

$$\% \text{ error of all sub-samples} = \sum x / 5$$

Table 2:4. Results from subsampling of 5 randomly selected samples from the summer field survey. Total abundance is given for 20% of the sample and for the remaining 80% of the sample. Total abundance is per 5 litre sample pumped from the hyporheic using a BOU-ROUCHE pump.

Sample	Sub sample	Chironomidae	Ostracoda	Harpacticoida	Cyclopoida	Macro-invertebrate	Acari	Oligochaetae	Sub sampling accuracy (%)
Wharfe	20%	19	1	10	3	1	2	3	+3.08
	80%	91	1	41	4	2	9	2	
Wharfe	20%	9	2	3	2	0	3	5	+9.20
	80%	40	7	14	1	3	1	19	
Derwent	20%	13	2	8	16	0	1	3	+6.05
	80%	55	2	28	67	1	1	5	
Frome	20%	7	2	1	0	3	0	3	+10
	80%	25	1	0	0	13	0	17	
Dove	20%	2	1	2	2	1	0	3	+5.45
	80%	17	1	5	5	3	0	10	
Total sub-sampling accuracy (%)									+6.76

The samples were sorted using a Bogorov sorting tray under a Nikon DM-10 stereomicroscope and all the sorted samples were photographed at calibrated magnifications. The length (l) and width (w) of all organisms (except Oligochaeta and Nematoda) were measured to the nearest micrometre using pre-taken photographs at pre-set calibrated magnifications using an image analyser. If large groups of similar sized instars were found (>50) then 20% of the sample was measured to calculate a mean, then the total number of individuals were counted and given the sub-sampled mean value. This process was primarily used for *Bryocamptus* sp. and Chironomidae larvae where abundances of the same instar were greater than 50. In order to calculate the volume of each species a prolate ellipsoid volume was used. Prolate ellipsoid volumes are suitable for fauna found in the hyporheic zone, where body width has been found to be more important than body length as depth increases into the sediments (Omesova et al. 2008). The prolate ellipsoid volume is calculated using the formulae:

$$V = 4/3\pi lw^2$$

(Where, w = width, l = length, V = volume (mm³))

After removal of organisms from the sample, the remaining material was dried at 40⁰C for 24 hours then weighed and ashed in a muffle furnace at 350⁰C for 4 hours to ascertain the loosely associated organic matter (LOM). LOM gives a rough approximation of the organic material associated with the sediment within each sample (Pusch and Schwoerbel 1994). The fauna collected were identified to species level where possible in particular crustaceans and macroinvertebrates. Oligochaetae, Diptera, Ostracoda and Nematoda were assigned to groups due to the poor preservation of Oligochaeta and Nematoda and also the predominance of early instar Chironomidae larvae which could not be identified accurately to a higher taxonomic level. The taxon-specific keys used for identification of fauna were: Copepoda (Einsle 1993, Janetzky et al. 1996); Cladocera (Scourfield 1994); Macroinvertebrates (Holland 1972, Elliott and Humpesch 1983, Hynes 1993, Wallace et al. 2003, Edington and Hildrew 2005) and Groundwater Crustacea (Gledhill 1993).

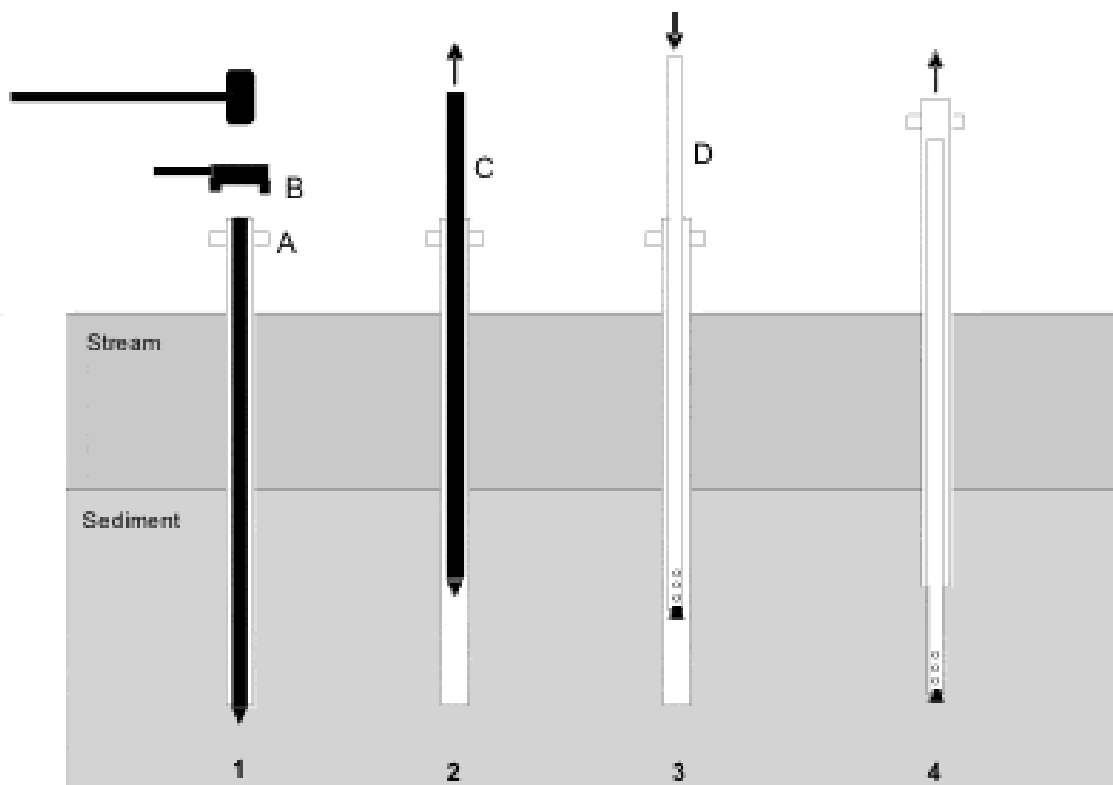


Figure 2:3. Stages in the installation of minipiezometer hydrometric investigations of up and downwelling: Driver mechanism consisting of solid steel driver rod (C) and steel outer casing with flange (A) hammered into sediment depth 30cm using a hammering cap (B). Driver rod (C) removed with the steel outer casing retained. Minipiezometer inserted into the outer steel casing. Outer steel casing removed with minipiezometer held in position (Baxter et al. 2003).

Physicochemical sampling

Vertical hydraulic gradient

To measure the vertical hydraulic gradient (VHG) a sharpened metal rod is inserted into a steel tube and hammered into the substrate to a depth of 30cm. After insertion the metal rod is removed leaving the steel tube remaining in the sediment. The mini-piezometer is then inserted into the steel tube which is also removed leaving the mini-piezometer inserted in the riverbed sediments (Fig. 2:3). Once the mini-piezometer is in place any stream water in the PVC tube is bailed using a pump and then left to settle for 2 hours. The water measurements taken are the distance from the top of the mini-piezometer to the water level in the mini-piezometer (h_p), the distance the mini-piezometer rises above the water surface (h_s) and the depth of the mini-piezometer in the sediment (L) (Baxter et al. 2003). VHG is a dimensionless unit as the denominator and numerator are the same and cancel out, positive values indicate upwelling, and negative values indicate downwelling. Vertical hydraulic gradient (VHG) is calculated as follows:

$$\text{VHG} = (h_s - h_p) / L$$

Water chemistry

Electrical conductivity, dissolved oxygen (DO), temperature and pH of both surface and hyporheic water were measured in the field using portable meters (pH - Hanna HI-9025; electrical conductivity - Hanna HI-9635; dissolved oxygen - temperature - Hanna HI-9145). Hyporheic physicochemistry measurements were taken directly from each piezometer. Surface water physicochemistry measurements were taken at the head of each riffle directly from the stream. A volume of hyporheic water (0.1 litre) was withdrawn from the piezometer and a volume of surface water (0.1 litre) was collected for later analysis of ion chemistry and frozen on the day of collection. Analysis of cations and anions was performed using high performance anion-exchange chromatography (HPLC), collected water samples were

defrosted on the day of analysis. Prior to analysis water samples were passed through a 0.7µm filter to remove particulate matter. Assay sensitivity of the HPLC equipment was 1ppm with the lower limit of ion detection 0.1ppm (Dionex., 2006).

Granulometry

Sediment samples were collected from the head of each riffle during the winter sampling campaign. Samples were collected to a depth of 20cm using a trowel and spade with collected sediment emptied into a 100µm mesh sample net placed slightly downstream from the sample area. The collected sample was then placed in a plastic bag for later analysis. Prior to analysis sediment samples were air dried in a tray for 1 week. When dried the sediment sample was weighed to the nearest gram to give the total sediment mass. The sediment sample was then fed into a sediment shaker; this consisted of 9 sieves corresponding to the phi-scale -4 to 4. The sediment was shaken for 20 minutes and then each sieve sample weighed to give a percentage of the total sediment mass. The sediment fractions were then plotted on a cumulative frequency curve with the cumulative percentage of sediment passed through the sieves plotted against the phi scale (4 to -4) (Krumbein and Sloss, 1951).

Cumulative percentage weight of sediment passed through each sieve (phi scale -4 to 4) is calculated:

Cumulative % passed of sieve (i.e. phi scale -4) = (sieve mass (sieve /total mass) * 100

At 50cm depth removal of sediment samples was not possible. To assess granulometric conditions at 50cm depth the time taken to pump 5 litres of water was recorded giving an indication of hydraulic conductivity properties of the hyporheic sediments. The longer it takes to pump a 5 litre sample of hyporheic water the greater the proportion of fine sediment in the hyporheic zone. The measure of hydraulic conductivity is a valuable tool to describe

the granulometric conditions present in the sub-surface environment (Descloux et al. 2010) with a strong relationship between hydraulic conductivity and sediment grain size (Sharp 1988).

Data analysis

Data analysis methods are given separately at the beginning of each relevant chapter

Chapter III: The influence of hydrogeology on the physicochemistry of the hyporheic zone

Abstract

Hydrogeology has a strong influence on the physical and chemical characteristics of the hyporheic zone and also on the river ecosystem. Upwelling groundwater dominates in deep sedimentary layers with surfacewater dominant in upper sedimentary layers. Across different hydrogeological settings the mixing layer and associated properties can vary in length (vertically, horizontally), by season (groundwater level) and geology (sediment composition), with these interactions manifested in distinct hyporheic habitats. This study looked at a range of hydrogeological types (specifically related to sediment composition) and described the dominant physicochemical patterns occurring in their hyporheic zones. Fine grained hyporheic sediments (i.e. Chalk) exhibited low values of hydraulic conductivity and coarse grained hyporheic sediments (i.e. limestone) had high values of hydraulic conductivity. High levels of dissolved minerals were a characteristic of the chalk hyporheic with low levels of dissolved minerals in the limestone hyporheic. Strong seasonal patterns were evident with conductivity and dissolved mineral concentrations lower during the winter across all river catchments except on the Chalk geology. Evidence of groundwater dominance was observed during both summer and winter in the Chalk hyporheic at 50cm depth with mineral concentrations increasing during the winter. Chalk streams exhibited weak vertical hydraulic gradients (VHG) at the head and tail of riffles. VHG patterns across other geologies were strong with downwelling water at the head of riffle and upwelling water at the tail. Vertical patterns in physicochemistry were evident across all river catchments except the Frome (chalk) with pH and dissolved oxygen (DO) significantly lower at 50cm than 20cm depth. In the chalk catchments (Frome and Piddle) dissolved minerals were significantly higher at 50cm than 20cm depth (Frome) or similar at both depths (Piddle). These results show clearly the effect sediment size has on water flow within the hyporheic and importantly how fine sediments can dampen surfacewater influence in the hyporheic zone. Regulation of hyporheic exchange processes results in chemically distinct environments both within and between river ecosystems influencing biological, physical and chemical processes in the hyporheic zone.

Introduction

The hyporheic zone is described as a critical component of whole stream ecosystems, particularly the role that the hyporheic zone plays in biogeochemical cycling of stream solute loads i.e. nutrient cycling (Dahm et al. 1998, Chestnut and McDowell 2000). High resolution studies are often undertaken at the reach scale, describing flowpaths through bedform features and interactions between streamwater and bed sediments (Hannah et al. 2009, Ingendahl et al. 2009, Soulsby et al. 2009). Describing hyporheic flowpaths and exchange processes along single reaches has contributed greatly in understanding the role the hyporheic zone plays within stream ecosystems. The difficulty has been in the application of knowledge across different stream types in particular stream types with different hydrogeological properties (Williams et al. 2010, Wondzell 2011). The hyporheic zone is described as a dynamic ecotone (Gibert et al. 1990) with the size of the ecotone dependent on sediment characteristics, with sediment size regulating exchange processes between surfacewater and groundwater. Hyporheic exchange processes between surfacewater and groundwater are scale dependent and controlled at the catchment scale by features such as geology and elevational gradients (Burkholder et al. 2008) or at the reach scale by alluvial sediment and bedform features (riffles, glides, runs) (Tonina and Buffington 2007, Arnon et al. 2010). Hyporheic exchange influences the characteristic chemical signature associated with each river system (Morrice et al. 1997).

Large scale exchange processes associated with groundwater flow are responsible for the baseline chemical signature of groundwater and surfacewater (see Chapter1, p27 for baseline definition). This chemical signature is derived through chemical and biochemical interactions between groundwater and the geological properties of soils and rocks (Valett et al. 1996). Deviations from baseline water quality are due to anthropogenic input of additional chemicals to the system primarily in the form of nutrients and pesticides (Robson and Neal 1997, Shand et al. 2007). Seasonality also influences the baseline chemistry of

streams and rivers. During summer rivers are often dominated by baseflow and consequently contain high concentrations of dissolved minerals. Concentrations of minerals are then reduced during winter as surfacewater from runoff becomes increasingly important to the system (Laudon and Bishop 2002, Lapworth et al. 2009).

Small-scale exchange processes occurring at the reach scale are determined by local geomorphological features such as variations in slope and depth, riffle-pool sequences, sediment size and changes in flow direction (i.e. meanders, boulders) (Brunke and Gonser 1997, Harvey and Wagner 2000). In riffle-pool sequences, downwelling water at the head of the riffle (high pressure zone) can travel considerable distances through the subsurface if conditions are suitable (i.e. through coarse grained materials) (Brunke and Gonser 1997) eventually upwelling at the tail of riffle (low pressure zone). The degree of up- and downwelling at the head and tail of riffles is related to riverbed permeability (sediment size), consequently riverbeds with a high proportion of coarse sediments can be highly dynamic (Vervier et al. 1992, Plenet and Gibert 1995, Song et al. 2007).

The hyporheic zone contains steep physicochemical gradients and the water is a mixture of surfacewater and groundwater (Bencala 1993, White 1993). Gradients occur vertically (groundwater-surfacewater), horizontally (riparian zones-surfacewater) and longitudinally through bedform features (i.e. riffles, runs) (Williams et al. 2010). Residence time of water in the hyporheic zone is controlled by capillary action; fine sediments characteristically exhibit low hydraulic conductivities and coarse sediments high hydraulic conductivities (Hiscock 2007). As the residence time of water passing through hyporheic sediments increases oxygen concentrations decrease due to oxygen uptake by microbial biofilms on the sediment surface (Pusch et al. 1998, Storey et al. 1999). In riffle features, downwelling surfacewater at riffle heads is characteristically high in dissolved oxygen relative to the tail. Conversely, dissolved minerals and electrical conductivity can be higher in riffle tails where upwelling water occurs (Stanford and Ward 1993, Williams et al. 2010)

As downwelling surfacewater flowpaths increase in length, levels of dissolved oxygen will reduce and dissolved minerals increase. Reduced oxygen can promote a switch to anaerobic respiration by microbial biofilms and have a major impact on chemical and biochemical processes occurring in the hyporheic zone (Malard and Hervant 1999, Baker et al. 2000). The use of alternative electron acceptors such as nitrate result in denitrification processes occurring in the hyporheic zone (Tiedje 1988, Pretty et al. 2006), a process of particular importance in many agriculturally impacted river catchments (Duff and Triska 1990, Triska et al. 1993, Hill 1996) and makes the understanding of physicochemical patterns in the hyporheic zone of particular importance.

In the UK, the hyporheic zone is poorly studied particularly across spatially large and hydrogeologically diverse areas. Supplementary knowledge is required to support findings on continental Europe (Dole-Olivier 1998, Marmonier et al. 2010), North America (Kasahara and Hill 2006, Song et al. 2007) and Australia (Boulton and Foster 1998, Boulton et al. 2003b). This study examines the physicochemistry of river catchments across a range of geologies increasingly resistant to weathering and different sediment characteristics (i.e. chalk – fine sediment size; sandstone – intermediate sediment size; limestone – coarse sediment size). The following hypotheses were tested:

- (1) River catchments on geologies resistant to weathering will contain coarse alluvial sediments. Consequently, water flow (hydraulic conductivity) within the alluvial sediments will be high, dissolved minerals low (weathering rates) and dissolved oxygen concentrations high. Therefore, electrical conductivity will be low in the limestone river catchments (resistant to weathering) and high in the chalk river catchments (easily weathered).
- (2) Seasonality will influence physicochemistry with baseflow during summer resulting in water high in dissolved minerals and low in oxygen with the reverse true in winter.

- (3) River catchments with fine alluvial sediments will exhibit a weakly connected hyporheic zone and up- and downwelling patterns at the head and tail of riffles will be undynamic. Patterns of water flow will become more dynamic as hydraulic conductivity increases and the proportion of coarse sediment in the hyporheic zone increases.
- (4) Physicochemical differences between the head and tail of riffle habitats (i.e. high DO and low electrical conductivity at the head of riffle low; DO and high electrical conductivity at the tail of riffles) will be higher on geologies with a dynamic and highly connected hyporheic zone (limestone) and lower at geologies with an undynamic and poorly connected hyporheic zone (chalk).
- (5) Physicochemical differences between depths will be less in river catchments with coarse alluvial sediments. Dissolved oxygen concentration would decrease from 20 to 50cm depth. Electrical conductivity and dissolved mineral concentrations will increase from 20 to 50cm depth.

Methods

Study site

River catchments located on different geological materials will have a range of hydraulic conductivity and porosity values related to sediment size (Hiscock 2007). Geological materials chosen for this study are chalk, limestone and Permo-Triassic sandstone. Rivers located on chalk catchments have fine alluvial river sediments derived from the fine grained chalk geology, whereas rivers located on limestone geology have coarse alluvial sediments with the local geology more resistant to weathering. Limestone geologies were also chosen north and south of the southern extent of the Devensian glacial limit. The sandstone geologies have fine to medium grained alluvial sediments. Riffles were selected in each river

catchment on 3rd to 4th order streams with similar bank widths and water depths. Refer to main methods section for detailed site description (Chapter 2).

Two river catchments were chosen from chalk and sandstone geologies. Two river catchments were selected on limestone to the south of the maximum extent of the Devensian glaciation and an additional two catchments were selected on limestone to the north of this limit. Thus eight catchments were selected in total. Within each river catchment four riffles were chosen and each riffle was sampled during summer (July 2009) and winter (November 2009). During the summer survey, samples were taken at the head and tail of each riffle at depths of 20cm and 50cm. Three replicates were taken at each depth. Distance between replicate samples was at least one metre with samples spread across the riffle head and tail. This sample collection was repeated during the winter survey although samples were only taken from 50cm depth.

Summer sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 2 depths = 384 samples.

Winter sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 1 depth = 192 samples.

Refer to main methods section for detailed site description (Chapter 2).

Physicochemical sampling

Vertical hydraulic gradient

Vertical hydraulic gradient (VHG) was measured by installing three mini piezometers across the head and tail of the riffle (see Chapter 2 for detailed methods). VHG is calculated by measuring the distance from the top of the piezometer to the water level in the tubes (h_p), the distance the piezometer rises above the water surface (h_s) and the depth of the piezometer in

the sediment (L) (Baxter et al. 2003). VHG is a dimensionless unit as the denominator and numerator are the same and cancel out with positive values an indication upwelling and negative values an indication of downwelling. Vertical hydraulic gradient (VHG) is calculated as follows:

$$\text{VHG} = (h_s - h_p) / L$$

Water chemistry

Electrical conductivity, dissolved oxygen (DO), temperature and pH of both surface and hyporheic water were measured in the field using portable meters. Hyporheic physico-chemistry measurements were taken directly from the piezometer. Surface water physico-chemistry measurements were taken at the head of each riffle directly from the stream. A volume of 0.1 litre of hyporheic water was withdrawn from the piezometer and a volume of 0.1 litre of surface water was also collected for later analysis of ion chemistry. Water samples for ion chemistry analysis were frozen on the day of collection. Analysis of cations and anions was performed using high performance anion-exchange chromatography (HPLC), with collected water samples defrosted on the day of analysis. Water samples were passed through a 0.7µm filter prior to analysis. Assay sensitivity of the HPLC equipment was 1ppm with the lower limit of ion detection 0.1ppm (Dionex. 2006)

Granulometry

Sediment samples were collected using a spade and 100µm mesh net and taken from the head of each riffle during the winter sampling campaign. The sediment samples were air dried in a tray for 1 week prior to sorting. The sediment sample was then fed into a sediment shaker consisting of 9 sieves corresponding to the phi-scale -4 to 4. The sediment was shaken for 20 minutes and then each sieve sample weighed to give a percentage of the total sediment mass. The sediment fractions were then plotted on a cumulative frequency curve with the

cumulative percentage of sediment passed through the sieves plotted against the phi scale (4 to -4) (Krumbein and Sloss 1951)

To assess granulometric conditions at 50cm depth the time taken to pump 5 litres of water was recorded giving an indication of the hydraulic conductivity properties of hyporheic sediments. The measure of hydraulic conductivity is a valuable tool to describe the granulometric conditions present in the sub-surface environment (Descloux et al. 2010) with a strong relationship between hydraulic conductivity and sediment grain size (Sharp 1988).

Refer to main methods section for detailed sampling methods (Chapter 2).

Data analysis

Ordination

Principal component analysis was used to identify the structure of the main environmental gradients sampled in this study. The use of PCA is suitable for linear rather than unimodal data and is particularly applicable for environmental data. PCA will identify the principal components (i.e. the environmental parameters that best explain variation in the dataset). Eigenvalues are calculated which explain the percentage proportion each axis contributes to explaining variation in the dataset. Separate analysis was performed for the summer dataset at both 20 and 50cm depth and the winter dataset at 50cm depth. In this analysis site and species scores were scaled symmetrically by the square root of the eigenvalues. Temperature was measured though not included in the analysis due to temporal differences in sample collection making comparisons unsuitable. Temperature can vary considerably over short temporal periods which in this study were up to one month. Other environmental variables will change, though to a lesser degree being related to local geology or seasonality.

Mixed model

The predictors in this experiment were depth, head and tail of riffle, riffle and geology. The responses tested were water chemistry (Na, K Mg, Ca, Cl, NO₃, SO₂, LOM, pH, electrical conductivity and hydraulic conductivity (pump time)). All statistical analyses were performed with R version 2.11.12 (R Development Core Team, 2010). The effect of predictors on responses was tested using linear mixed effect models. Prior to analysis data exploration was conducted to identify possible outliers in the response and explanatory variables. Normality was checked using graphical plots and deviations from normality were corrected using log₁₀(n+1) transformations where appropriate. Residuals were plotted after model building to check for any violation of heterogeneity (Zuur et al. 2009).

Variations in chemical and physical hydrogeology between and within river catchments were tested using linear mixed effects models (LME). The use of LME models accounted for the hierarchical nature of the experimental design, with depth nested in riffle head and tail (UD), UD nested within riffle, and riffle nested in river catchment. Mixed models allow for the use of both fixed and random effects in the study design. The following variables were fitted as fixed effects in the between catchment analyses: river catchment, with riffle fitted as random effect. The within catchment analysis: depth and UD were fitted as fixed effects, with riffle fitted as a random effect. Restricted maximum likelihood method was used to estimate error terms. Models were chosen using Akaike Information Criteria (AIC) scores, the score closest to zero being the model with the best fit. The model selection process begins by starting with a Generalised Least Squares (GLS) full model with all interactions and no random effect. The use of GLS models will account for correlation of errors and unequal variances. The full model was compared to a mixed model containing a random intercept, a random intercept and slope and a random effects model and the model with the lowest AIC score was chosen. Non-significant interactions were removed from the model in a stepwise approach beginning with the full model including all interactions. After each model reduction the previous and

current model were compared using analysis of variance (ANOVA). If the difference between the models was not significant then no explanatory power is lost in the reduced model and we can then proceed to the next model building step and reduce the model further until parsimony is reached (Zuur et al. 2009). Linear mixed effects models were performed using the package “nlme” version 3.1-102 (Pinheiro 2011).

Results

Variation in physicochemistry between river catchments of different hydrogeological properties

Summer survey - 20cm depth

The 1st and 2nd axes of 11 environmental variables measured explained 55.1% of the variance of the environmental dataset; eigenvalues were 0.354 (1st axes) and 0.196 (2nd axes), 3rd and 4th PCA axes were 0.146 and 0.096 respectively (Fig 3.1a). The 1st PCA axis was positively related to potassium and reflected an electrical conductivity gradient. The 2nd axis was positively related to DO and reflected a biological gradient with DO inversely related to organic matter (Fig. 3:1a). The 3rd and 4th axes were positively related to magnesium and nitrate, respectively.

The carboniferous limestone sites in the Yorkshire Dales were projected onto the negative end of the 1st axes. Low concentrations of dissolved minerals and low electrical conductivity resulted in low PC1 scores. PC2 scores for the Dales sites were mostly positive with DO and pH both high, with site specific variability in physicochemistry small with all sites tightly clustered reflecting similar physicochemical profiles. The carboniferous limestone sites in the Peak District were projected onto the positive end of the 1st axis with strong correlations with magnesium, sodium, sulphate and potassium with the majority of PC1 scores positive. The majority of PC2 scores in the Peak District were also high and positive with pH and DO concentrations high. Variability in physicochemistry was evident between the Yorkshire

Dales and Peak District sites, primarily due to high concentrations of dissolved minerals in the hyporheic water of the Peak District.

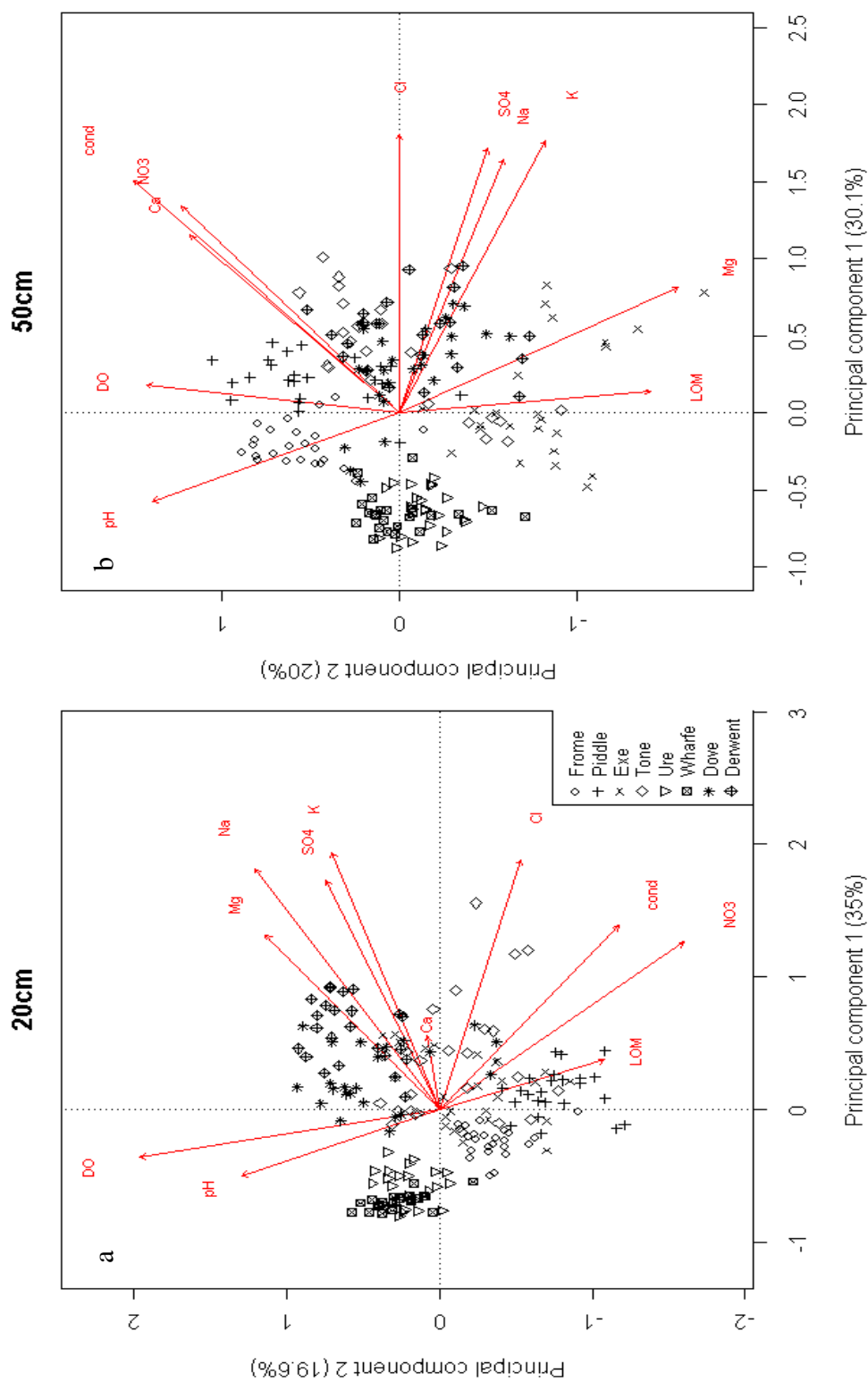


Figure 3.1. Principal component analysis of hyporheic physicochemistry (n = 384) collected during the summer survey summer (July) 2008. Study sites were sampled from a depth of 20cm (a) (n = 196) and 50cm (b) (n = 196).

Considerable site specific variability in physicochemistry was evident at the Permo-Triassic sandstone sites. Many sites were clustered around the origin with low PC1 scores (both positive and negative) indicating an undifferentiated distribution. PC1 scores were high at two sites at the Tone catchment (Hillifarance Brook and the River Tone at Runnington) due to high chloride concentrations at both sites. PC2 scores for the Tone and Exe river catchments were low (both positive and negative) reflecting an undifferentiated distribution.

The chalk sites in Dorset showed little site specific variability in physicochemistry with sites tightly clustered with similar physicochemical profiles. PC1 scores for both chalk sites were low with an undifferentiated distribution along the 1st axis. Chalk sites were projected to the negative end of the 2nd axis. PC2 scores were high and negative for both the Frome and Piddle sites due to low DO concentrations.

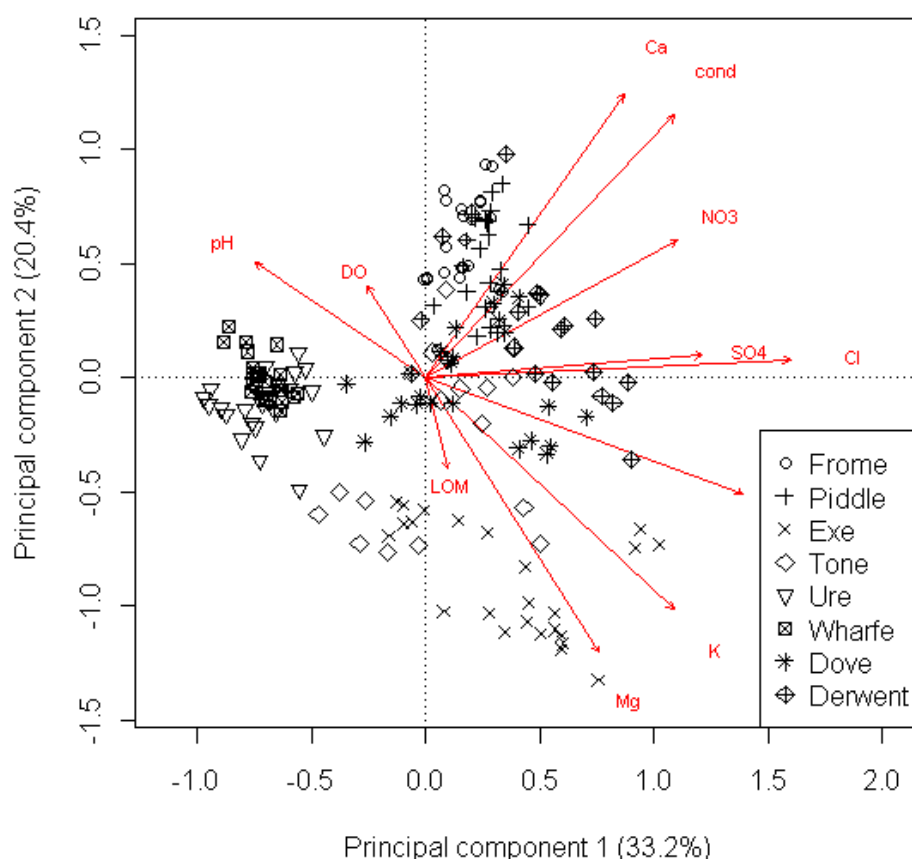


Figure 3.2. Principal component analysis of hyporheic physicochemistry at 50cm depth (n = 196) collected during the winter survey (October-November) 2008.

Summer survey - 50cm depth

The 1st and 2nd axes of the 11 environmental variables measured explained 50.1% of the variance of the environmental dataset; eigenvalues were 0.311 (1st axes) and 0.201 (2nd axes), 3rd and 4th PCA axes were 0.148 and 0.091 respectively (Fig 3.1b). The 1st PCA axis was positively related to chloride and reflected an electrical conductivity gradient (Fig. 3.1b). The 2nd PCA axis was positively related to DO and reflected a biological gradient with DO inversely related to organic matter. The 3rd and 4th axes were positively related to nitrate and LOM, respectively.

The carboniferous limestone sites in the Yorkshire dales were projected onto the negative end of the 1st axis with low PC1 scores. Low concentrations of dissolved minerals and low electrical conductivity are characteristic of the Yorkshire Dales sites with sites tightly clustered with similar physicochemical profiles. PC2 scores were low and both positive and negative due to clustering around the origin of the 2nd axis giving an undifferentiated distribution. The carboniferous limestone sites in the Peak District exhibited considerable site specific variability with sodium, sulphate and potassium high across some sites. Sites were projected to the positive end of the 1st axis with PC1 scores high, although four sites on the River Dove in Dovedale had negative PC1 scores due to low concentrations of dissolved minerals at the site.

The Permo-Triassic sandstone sites showed variability in physicochemistry between sites. The two rivers in the Tone catchment (Hillifarance Brook and the River Tone at Runnington) had high PC1 scores due to high chloride concentrations. Most PC1 scores were positive apart from the Tone at Greenham with negative PC1 scores due to low concentrations of dissolved minerals. PC2 scores for the Tone sites varied considerably with scores both positive and negative. The Tone at Greenham had very low PC2 scores due to low DO concentrations at the site. PC2 scores for the other Tone sites were small with sites close to the origin of PC2 giving an undifferentiated distribution along the 2nd axis. PC1 scores for

the River Exe sites were low and clustered around the origin of PC1 giving an undifferentiated distribution. PC2 scores for the Exe were high and negative due to low DO concentrations at 50cm depth.

At both chalk sites PC1 scores were low and clustered around the origin of PC1 giving an undifferentiated distribution along the 1st axis. The majority of PC2 scores for the Frome and Piddle were positive and high due to DO concentrations in the chalk hyporheic (50cm depth) being relatively high. The chalk hyporheic exhibited diametrically opposite patterns at 20 and 50cm depths along the 2nd axis. Sites were projected to the negative end of the 2nd axis at 20cm depth and inversely related to DO. The pattern reverses at 50cm depth with the chalk sites projected to the positive end of the 2nd axis and directly related to DO.

Winter survey – 50cm depth

The 1st and 2nd axes of the 11 environmental variables measured at 50 cm depth from the 196 sites explained 53.6% of the variance of the environmental dataset; eigenvalues were 0.332 (1st axes) and 0.204 (2nd axes), 3rd and 4th PCA axes were 0.107 and 0.095 respectively (Fi 3.2) . The 1st PCA axis was positively related to chloride. The 2nd axis was positively related to electrical conductivity (Fig. 3:2). The 3rd and 4th axes were associated with LOM and DO respectively.

The carboniferous limestone sites of the Yorkshire Dales were projected towards the negative end of the 1st axis. PC1 scores for both Yorkshire Dales sites were high and all negative due to low concentrations of dissolved minerals and low electrical conductivity. PC2 scores for the Yorkshire Dales sites were all low with sites clustered above and below the PC2 origin. All sites in the Yorkshire Dales are tightly clustered with similar physicochemical profiles. The Peak District sites were mainly projected to the positive end of the 1st axis with PC1 scores high, primarily due to high concentrations of sodium, sulphate and potassium. The sites on the River Dove had negative PC1 scores with lower

concentrations of dissolved minerals at this site. PC2 scores were more variable (both positive and negative) with scores mainly low with many sites close to the PC2 origin giving an undifferentiated distribution.

The Permo-Triassic sandstone sites showed considerable site specific physicochemical variability. PC1 scores on the River Exe were all positive (except River Lowman site) with high PC1 scores displaying a strong correlation with magnesium. The Exe sites were projected close to each other with physicochemistry similar across the sites. PC1 scores for the Tone sites were positive and low with many sites close to the PC1 origin, indicating an undifferentiated distribution along the 1st axis. PC2 scores for the Tone displayed considerable site specific variability. PC2 scores for the two sites on the River Tone at Greenham and Runnington were high and negative with conductivity low at these sites.

The chalk sites displayed little variability along the 1st axis with PC1 scores low and positive. PC2 scores for both the Frome and Piddle were high and positive with electrical conductivity and calcium high in the hyporheic zone of both chalk rivers. The chalk sites were also again directly related to DO and inversely related to LOM replicating results from the summer survey.

Variation in seasonal physicochemistry within river catchments of different hydrogeological properties

Physicochemical data from all river catchments is given in Appendix 1. The strongest pattern to emerge between high and low groundwater levels is the significant increases in dissolved oxygen concentrations across all catchments during the winter survey (Table 3:1). Patterns of pH displayed inconsistent patterns between high and low groundwater levels. In the two chalk catchments, pH was significantly higher in the Frome during significantly lower in the Piddle during the winter survey (Table 3:1). The two sandstone catchments (Exe and Tone) showed a consistent pattern with pH significantly higher in the hyporheic of both catchments

during the winter survey. In the limestone catchments the pattern was less clear with pH significantly higher in the Ure and significantly lower in the Derwent during the winter survey. No significant difference in pH levels was observed at the Wharfe and Dove catchments between the summer and winter surveys (Table 3:1). Patterns in electrical conductivity displayed strong patterns between summer and winter surveys with electrical conductivity significantly lower during the winter survey at the Exe, Tone, Ure, Wharfe and Dove catchments. Only in the Piddle and Derwent catchments was electrical conductivity significantly higher during the winter. No significant difference in electrical conductivity was observed at the Frome catchment between the summer and winter (Table 3:1).

In general, groundwater associated ions decreased during the winter survey. At the Ure and Wharfe catchments in the Yorkshire Dales this pattern was most apparent, all groundwater associated ions were significantly lower during winter reflecting the reduction in baseflow dominance in streams during winter (Table 3:1). This pattern was less evident in the Peak District limestone sites with magnesium and calcium significantly higher during the winter survey at both the Dove and Derwent catchments, respectively. Magnesium and calcium were also the only ions where no significant difference was observed at both the Dove and Derwent, respectively. All other ions at the Peak District sites were significantly lower during winter.

At the two sandstone river catchments groundwater associated ions were lower during the winter survey with sulphate and chloride in the Exe catchment and sulphate, chloride and calcium in the Tone catchment all significantly lower, no significant difference was observed for all other ions (Table 3:1). The Frome catchment was unusual with groundwater associated ions all significantly higher during the winter survey (Table 3:1). This pattern was not replicated in the Piddle catchment with only magnesium significantly higher and sulphate significantly lower during winter, all other groundwater ions showed no significant difference between seasons (Table 3:1).

Comparison	pH	DO	Cond	Cl	NO ₃	SO ₄	K	Na	Ca	Mg	LOM
Frome											
Season (1,43)	17.350***	25.955***	2.071	6.895*	12.902***	234.337***	0.655	7.692**	56.755***	46.425***	7.098*
Piddle											
Season (1,43)	9.255**	56.658***	14.846***	8.614	40.046***	21.199***	1.999	0.075	0.104	11.452**	0.002
Exe											
Season (1,43)	28.120***	291.865***	17.694***	4.605*	2.468	29.092***	11.668**	9.042**	3.783	3.714	5.557*
Tone											
Season (1,43)	10.101**	59.931***	62.758***	40.971***	13.833***	117.676***	6.601*	8.495	43.933***	1.657	0.942
Ure											
Season (1,43)	15.254***	67.846***	23.276***	167.135***	9.382**	234.339***	0.927	5.706*	6.242**	89.186***	1.559
Wharfe											
Season (1,43)	0.793	23.068***	62.758***	41.906***	9.717**	145.147***	5.013*	25.186***	18.975***	64.863***	2.256
Dove											
Season (1,43)	0.013	0.419	16.140***	3.619	9.701**	11.644**	53.033***	129.651***	0.028	22.162***	2.415
Derwent											
Season (1,43)	10.086**	15.655***	28.150***	3.908	22.080***	0.987	20.094***	36.266***	10.684**	1.619	1.905

Table 3.1. Linear mixed effects model of comparisons of physicochemistry results between seasons (summer and winter) at 50cm depth. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Season = sampling occasion (summer and winter), cond = electrical conductivity, LOM = loosely associated organic matter.

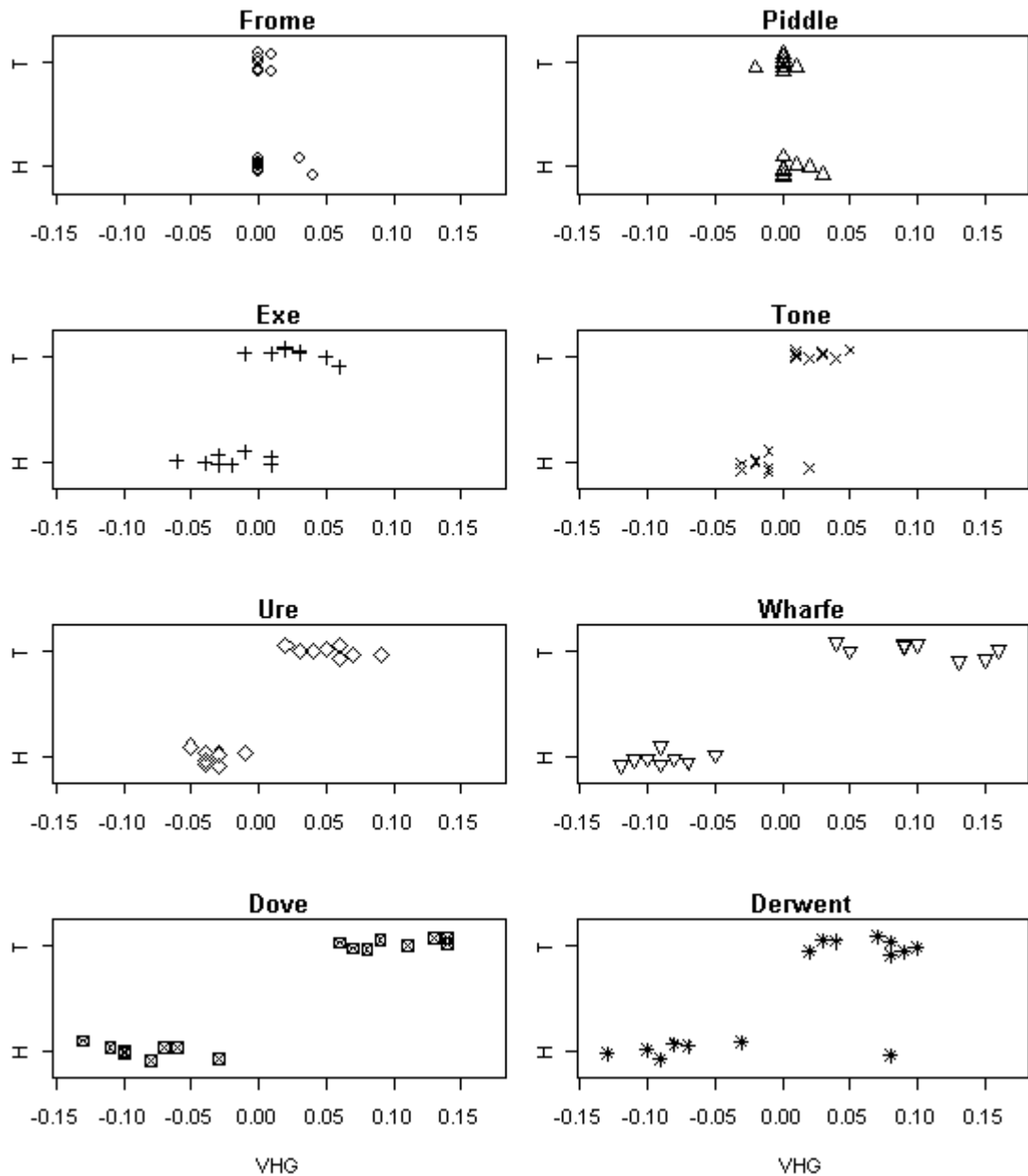


Figure 3.3. Vertical hydraulic gradient (VHG) measured at 30cm depth from the head (H) and tail (T) at riffles located on each river catchment. Positive VHG indicates upwelling subsurface water and negative VHG indicates downwelling surface water.

Table 3.2 Linear mixed effects model results of pump time compares between geological areas. Pump time was measured during the winter survey. Riffle was fitted as a random effect with river catchment and head and tail of riffle (HT) fitted as fixed effects.

	Degrees of freedom	F-value	<i>P</i> -value
River catchment	7,161	10.015	<0.001
River catchment x HT	7,161	1.334	0.230

Groundwater-surfacewater interactions: influence of hydrogeology on hyporheic water within riffle habitats

Vertical hydraulic gradient (VHG)

There was considerable variability across the catchments in the strength of vertical hydraulic gradients. The two chalk catchments displayed weak patterns of vertical water movement at the head and tail of riffles. Areas of downwelling were recorded at only one site on the Piddle, the majority of sites VHG was close to zero. Upwelling was observed in both chalk catchments though the pattern was random across both the head and tail of riffles. Vertical water movement was more apparent at the sandstone catchments with characteristic up- and downwelling zones observed at the head and tail of riffles, although at a few sites vertical water movement was weak. The carboniferous limestone areas of both the Yorkshire Dales and the Peak District were characterised by strong vertical water movement within the hyporheic zone, with characteristic patterns of up- and downwelling observed at the head and tail of the majority of riffles (Fig. 3:3).

Hydraulic conductivity

The time taken to pump 5 litres of water using the BOU-ROUCHE method was significantly higher at the two chalk river catchments (Frome and Piddle) in comparison to all other catchments (Table 3:2, Fig. 3:4). No significant difference in pump times was observed between the two chalk catchments with pump times similar. No significant difference in pump times was observed between the Exe, Tone, Ure, Wharfe, Dove and Derwent catchments. Pump times were not significantly different between upwelling and downwelling zones at each river catchment (Table 3:2).

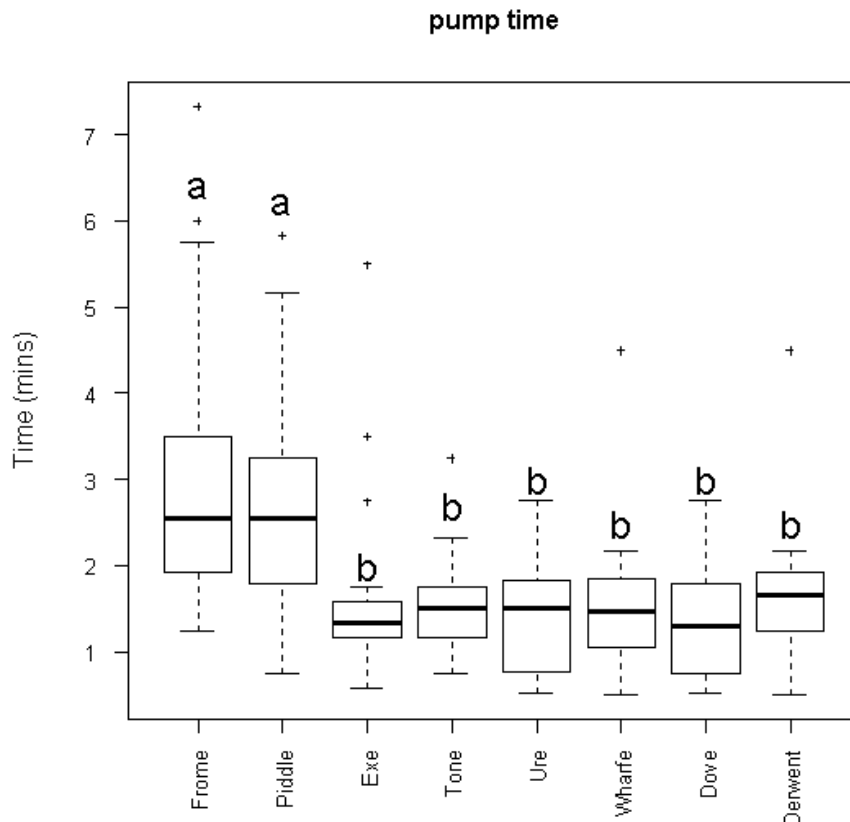


Figure 3.4. Boxplots of pump times measured at each geological catchment. Pump time is the time taken to extract 5 litres of water using a BOU-ROUCHE pump attached to a piezometer inserted at 50cm depth. Letters that are the same indicate no significant difference. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range.

Table 3.3. Granulometric results of benthic sediment collected from each riffle sampled in the survey (depth 20cm). Figures are percentage of total mass collected on each phi scale sieve. Size ranges and Wentworth description of sediment collected are given for each phi scale

PHI SCALE	4	3	2	1	0	-1	-2	-3	-4
Wentworth scale	Very fine sand	Fine sand	Medium sand	Coarse sand	Very coarse sand	Very fine gravel	Fine gravel	Medium gravel	Coarse gravel
Size range	62.5-125µm	125-250µm	¼-½mm	1mm	1-2mm	2-4mm	4-8mm	8-16mm	16-32mm
Frome	0.07	0.69	3.84	9.29	17.10	22.44	17.67	28.90	0
Piddle	0.04	0.33	1.86	11.14	22.99	13.92	16.20	33.52	0
Exe	0.11	0.52	1.34	2.47	7.29	15.39	29.71	43.18	0
Tone	0.21	0.54	3.29	14.20	9.89	18.73	30.35	22.80	0
Ure	0.13	0.57	2.61	7.02	14.66	20.09	18.82	36.08	0
Wharfe	0.21	0.53	1.55	5.30	16.07	16.42	20.09	39.84	0
Dove	0.33	1.37	3.82	7.41	9.10	12.77	24.47	40.73	0
Derwent	0.11	0.61	2.06	7.2	17.18	17.9	20.33	34.61	0

Granulometry

The results from the granulometric analysis of sediment extracted from the top 20cm of the hyporheic zone are shown in Table 3:3 and Figure 3:5. Very-fine sand (phi scale = 4) and fine sand (phi scale = 3) were in low proportions at all river catchments with total percentage values less than 1.5%. Medium sand (phi scale = 2) proportions were highest at the Frome and Dove river catchments, and coarse sand highest at The Frome, Piddle and Tone river catchments (phi scale = 1). The proportion of coarse sand was highest at both the Frome and Piddle catchments (phi scale = 0) with proportions at the Exe catchment low. At the Exe catchment the proportion of coarse sediments increased medium gravel (phi scale = - 3) proportionally highest at the Exe catchment. The amount of coarse sediments found in the Exe catchment is comparable to results found from the carboniferous limestone sites with all limestone sites containing high proportions of medium gravel (phi scale = -3). All sites had a high proportion of very fine, fine and medium sized gravel sediment (phi scale = -1, -2, -3) in comparison to finer sediments.

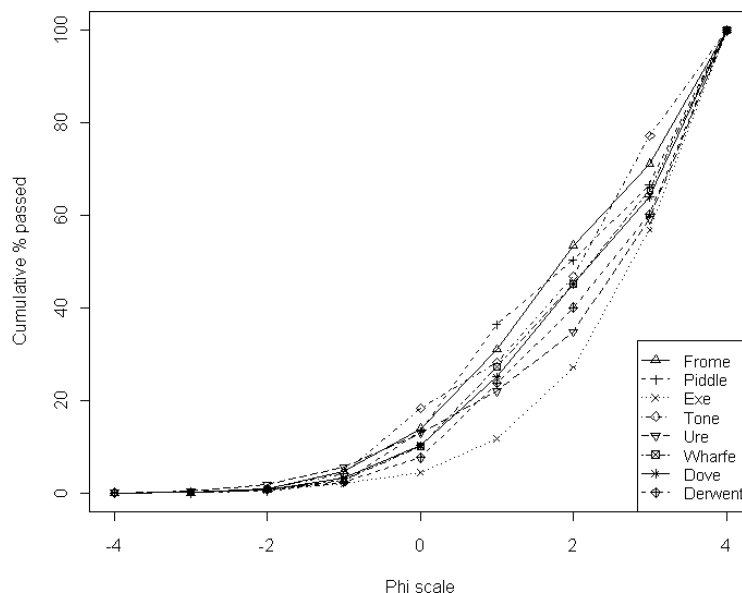


Figure 3.5. Cumulative percentage of sediment passed through vertically stacked sieves graded along the phi scale -4 to 4. Sediment samples collected from 20cm depth at the head of each riffle sampled (n = 32).

Summer survey

The results for differences in physicochemistry between the head and tail of riffles during the summer survey are given in Table 3.4. No significant difference in DO concentration was observed between the head and tail of riffles in six out of eight river catchments, the exceptions were the Wharfe and Dove where DO was significantly higher in the tail of the riffles. No significant difference in pH was observed between the head and tail of riffles in six out of eight river catchments, the exceptions were the Piddle and Wharfe with pH significantly higher in riffle tails. Potassium concentrations did not differ significantly between the head and tail of riffles in 5 out of eight river catchments. The exceptions were the Exe and Dove river catchments where potassium was significantly higher in the tail of the riffle and the Frome where the reverse pattern was observed. There was no significant difference in nitrate concentrations between the head and tail of riffles across all river catchments. In six out of eight river catchments no significant difference was observed in electrical conductivity between the head and tail of riffles. The exceptions were the Exe and Ure catchments where electrical conductivity was significantly higher in the tail of riffles.

The only catchment to show consistent patterns between the head and tail of riffles for groundwater associated ions was the Exe catchment with all ions significantly higher in the tail of the riffle in comparison to the head (Fig. 3.6). In six out of eight river catchments (Frome, Piddle, Tone, Ure, Wharfe and Dove) no significant difference was observed for all groundwater associated ions between riffle heads and tails. The one exception was the Derwent where sulphate and chloride concentrations were significantly lower in the tail than the head of the riffles.

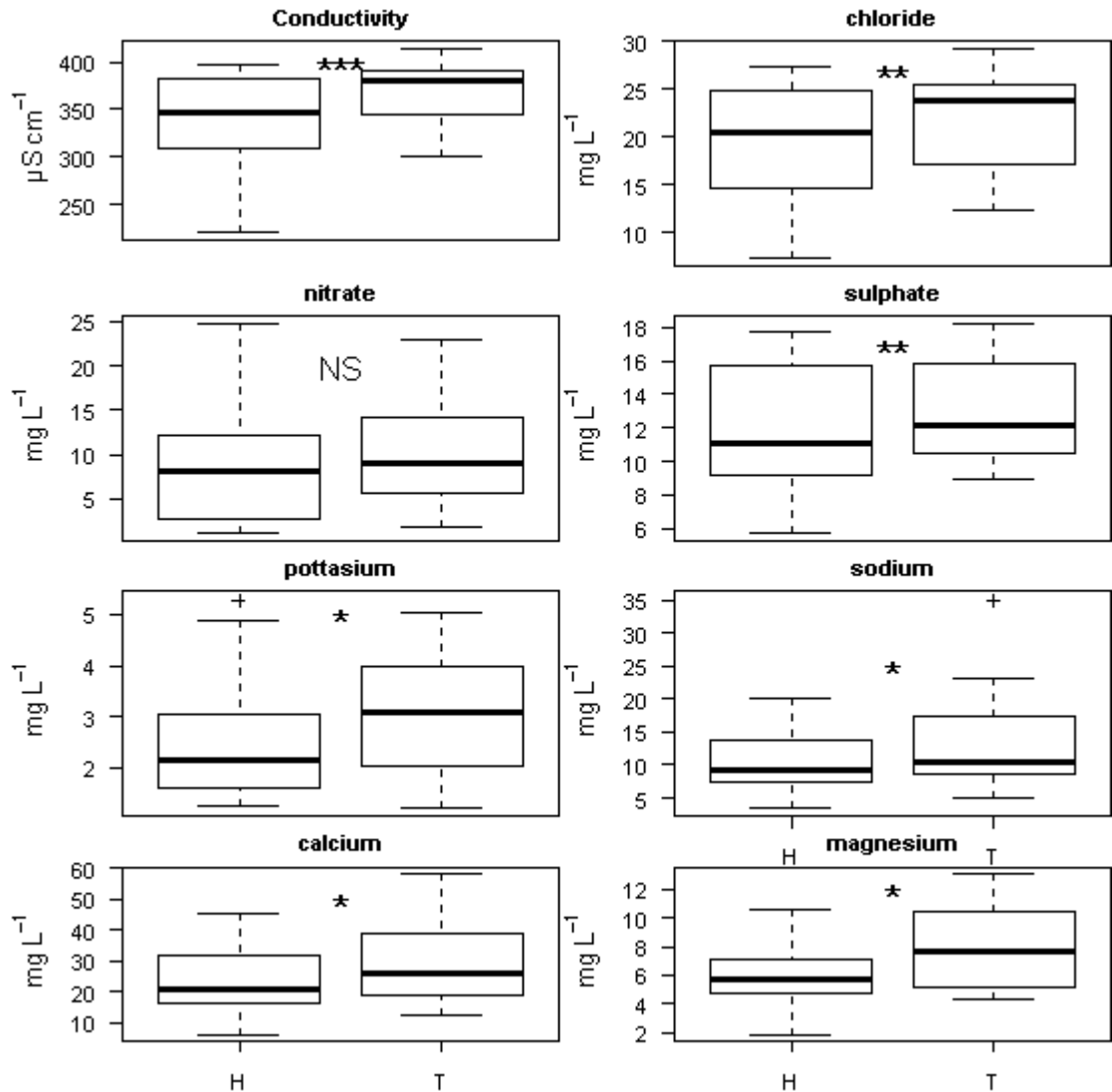


Figure 3.6. Differences in physicochemistry measured at the head and tail of riffles in the Exe river catchment, Devon. Data is presented from the summer survey, July 2009. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range.

Winter survey

There was little variability between the head and tail of riffles during the winter survey (Table 3:5). The strongest patterns were again observed at the Exe river catchment consistent with results from the summer survey. Electrical conductivity, nitrate and all groundwater associated ions apart from sulphate were significantly higher in the tail than the head of the riffle with no significant difference observed for sulphate. Dissolved oxygen, pH and

potassium did not differ significantly between the head and tail of riffles in the Exe catchment

Across the other river catchments no strong patterns were observed between the head and tail of riffles. Where significant differences were observed the pattern was for an increase in physicochemistry in the tail of riffles. All the following were significantly higher in the tail of riffles: magnesium in the Piddle catchment; electrical conductivity in the Tone catchment; pH in the Ure catchment and electrical conductivity and magnesium in the Dove catchment (Table 3:5). In the Wharfe and the Derwent this pattern reversed with pH and potassium significantly lower in the tail of riffles in the Wharfe and Derwent catchments respectively (Table 3:5). Notably in the Frome catchment there were no significant differences for all measured physicochemical variables between the head and tail of riffles (Table 3:5).

The influence of hydrogeology on physicochemistry in the hyporheic zone at 20 and 50cm depth

Dissolved oxygen levels and pH were significantly lower at 50cm than 20cm depth across all river catchments except the Frome (chalk). There was a weak interaction effect at the Frome between depth and head and tail of riffles due to DO higher at 50cm in the head of the riffle and lower at 50cm at the tail of the riffle (Table 3:4). At three out of five catchments (Frome, Dove and Derwent) no significant difference was observed in electrical conductivity between depths. Electrical conductivity was significantly lower at 50cm depth in both the Piddle and Exe, whereas in the Tone, Ure and Wharfe conductivity it was significantly higher at 50cm depth highlighting the variability across river catchments.

Table 3.4. Linear mixed effects model of comparisons of physicochemistry between: 1) head and tail of riffles (UD), 2) 20 and 50cm depths and 3) interaction between UD and depth from the summer sampling survey (2008) (* p < 0.05, **p < 0.01, *** p < 0.001

	Comparison	pH	DO	Cond	Cl	NO3	SO4	K	Na	Ca	Mg	LOM
Frome	UD _(i,4i)	3.11	0.09	1.66	0.448	1.092	0.123	5.396*	0.163	0.559	3.3	0.272
	Depth _(i,4i)	0.1	4.041	0.09	0.681	3.787	5.617*	5.396*	0.333	22.008***	36.800***	5.756*
	Depth _{UD_(i,4i)}	1.43	7.060*	0.8	3.669	5.426*	4.863*	3.898	0.013	0.432	2.172	0.881
Piddle	UD _(i,4i)	6.712*	3.142	1.17	3.327	0.24	2.516	0.618	0.943	2.446	0.168	1.368
	Depth _(i,4i)	15.353***	9.573**	13.526***	3.873	0.097	2.747	0.283	7.440**	16.195***	0.467	2.474
	Depth _{UD_(i,4i)}	0.038	0.3	9.174**	0.23	0.644	2.295	0.078	3.086	0.934	5.395*	1.462
Exe	UD _(i,4i)	0.001	0.387	15.953***	10.521**	2.289	7.767**	6.892*	4.951*	6.226*	10.150**	0.077
	Depth _(i,4i)	19.886***	137.002**	17.255***	0.463	8.226**	0.974	0.109	0.124	0.26	1.417	16.230***
	Depth _{UD_(i,4i)}	0.212	0.785	9.706**	0	0.045	1.348	0.22	1.075	1.916	4.631*	0.482
Tone	UD _(i,4i)	2.288	1.04	0.541	0.102	0	2.158	0.094	0.149	0.026	0.183	0.663
	Depth _(i,4i)	10.334**	35.599***	18.932***	0.204	0.054	2.253	2.355	1.24	56.169***	19.372***	4.610*
	Depth _{UD_(i,4i)}	4.121*	0.585	0.736	3.164	5.467*	3.313	0.001	0.007	2.113	2.777	7.104
Ure	UD _(i,4i)	0	3.563	9.361**	0.022	0.965	0.29	0.007	0.081	0.002	0.51	0
	Depth _(i,4i)	24.047***	117.686**	11.978***	19.487***	2.082	15.296***	1.231	1.371	0.006	0.111	2.198
	Depth _{UD_(i,4i)}	1	5.487*	3.827	0.677	1.747	0.123	3.013	0.009	0.025	0.51	0.208
Wharfe	UD _(i,4i)	5.177*	6.904*	3.87	5.032*	0.094	0.08	0.899	0.276	1.034	3.948	0.113
	Depth _(i,4i)	21.467***	29.280***	20.210***	7.458**	0.241	0.032	27.209***	3.572	0.408	2.325	22.069
	Depth _{UD_(i,4i)}	0.027	1.71	3.51	1.608	0.004	0.239	0.425	0.223	0.005	0.48	0.028
Dove	UD _(i,4i)	0.056	6.442*	3.197	0.467	2.52	0.004	6.042*	1.318	3.815	2.389	10.053**
	Depth _(i,4i)	8.258**	20.295***	1.992	0.01	0.165	2.55	0.082	2.635	7.694**	3.242	0.357
	Depth _{UD_(i,4i)}	0.166	0.487	0.284	0.11	1.607	0.192	4.894	1.707	1.597	0.66	0.475
Derwent	UD _(i,4i)	1.111	2.927	1.355	6.591*	1.576	7.36**	7.940**	1.265	0.031	0.125	7.785**
	Depth _(i,4i)	11.277**	16.928***	3.469	2.973	25.093***	2.205	0.031	2.33	7.025*	13.675***	10.814
	Depth _{UD_(i,4i)}	0.522	0.713	1.951	0.037	0.063	1.014	2.858	0.079	1.124	0.502	1.946**

Table 3.5. Linear mixed effects model results of comparisons of physicochemistry between the head and tail of riffles of each river catchment during the winter sampling survey (2008) at 50cm depth (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Comparison	pH	DO	Cond	Cl	NO ₃	SO ₄	K	Na	Ca	Mg	LOM
Frome _(1,19)	3.2	2.451	0.14	0.946	0.608	2.994	0.375	0.912	0.106	0.097	0.017
Piddle _(1,19)	2.114	0.074	1.5	0.028	1.824	0.655	0.845	2.515	0.319	6.888*	0.028
Exe _(1,19)	0.431	0.357	9.178**	6.120*	2.329	0.608	1.368	5.121*	6.802*	16.741***	0.563
Tone _(1,19)	3.67	2.196	3.031*	0.387	2.162	3.071	1.207	0.057	0.243	1.181	0.188
Ure _(1,19)	5.064*	1.947	2.304	0.531	0.722	0.796	0.434	0.201	1.781	0.789	0.239
Wharfe _(1,19)	12.231**	0.407	4.551*	0.791	0.004	0.636	0.053	1.453	0.289	3.97	1.39
Dove _(1,19)	0.031	1.211	4.791*	0.249	1.097	0.074	0.002	0.11	1.409	6.295*	0.235
Derwent _(1,19)	0.069	0.768	2.98	0.262	0.035	0.807	5.025*	4.137	3.785	0.39	0.468

In six out of eight river catchments no significant difference in potassium and nitrate concentrations was observed between depths. The exceptions were the Frome and Wharfe with potassium concentrations significantly higher at 50cm than 20cm and the Exe and Derwent with nitrate significantly lower at 50cm than 20cm depth. There was a significant interaction effect for nitrate in the Frome catchment with nitrate higher at 50cm in the head of the riffle and lower at 50cm in the tail of the riffle following a similar pattern to DO concentrations at the Frome (Table 3.4).

The groundwater associated ion concentrations in the two chalk catchments followed similar patterns with ion concentrations often higher at 50cm than 20cm depth. In the Frome, magnesium, calcium and sulphate concentrations were significantly higher at 50cm than 20cm depth; both chloride and sodium were not significantly different. In the Piddle, both calcium and sodium concentrations were significantly higher at 50cm than 20cm depth; magnesium, sulphate and chloride were not significantly different. In the Exe catchment all groundwater associated ions showed no significant difference between depths. In the Tone catchment magnesium was significantly higher at 50cm depth and calcium significantly lower at 50cm depth (Table 3.4).

In the limestone catchments patterns were also mixed, in the Ure only sulphate and chloride were significantly higher at 50cm depth and in the Wharfe only chloride was significantly

higher at 50cm depth. In the two Peak District catchments the Dove showed little variability with only calcium significantly higher at 50cm depth and the Derwent catchment only magnesium and calcium were significantly higher at 50cm (Table 3.4).

Discussion

Regional scale hydrological influences on hyporheic physicochemistry

The physicochemistry of groundwater fed rivers is defined by the complex interaction of local geology, hydrology and climatic factors (Morrice et al. 1997, Valett et al. 1997). Sediment size is an important determinant of the levels of solutes in the hyporheic zone due to its control on water flow (i.e. fine sediment – slow flow; coarse sediment – fast flow); with slow water flows increasing weathering rates and levels of dissolved minerals. Electrical conductivity levels rise with dissolved mineral concentrations, therefore, geological types with clay and clay-rich sediments (fine sediments) are easily distinguished from sands, sandstones and limestones (coarse sediments) (Zalasiewicz et al. 1985). My first hypothesis: that river catchments with distinct hydrogeological properties will be differentiated along an electrical conductivity gradient was partly supported. The highest electrical conductivity levels occurred in the chalk river catchments. Groundwater flow through chalk aquifers is primarily through channels with apertures ranging from a few millimetres wide to a few centimetres, with wider channels relatively rare (Waters and Banks 1997). Chalk aquifers have a large number of very small solutional channels (i.e. caused by dissolution of rock by water) with slow through flow times and subsequently high concentrations of dissolved solutes (Waters and Banks 1997).

The lowest electrical conductivity levels occurred in the Yorkshire Dales with low concentrations of dissolved minerals in the water, reflecting the quick through-flow time of groundwater in the catchment and geology also resistant to weathering. Water flow through carboniferous limestone in the Yorkshire Dales has been mapped extensively (Waltham et al.

1997), the solutional channels form a dendritic system with channel widths averaging 3m and varying from <1m in headwater areas to >10m where springs emerge at the surface. These solutional channels (conduits formed from dissolution of rock) occupy a small percentage of the total aquifer, sinking stream recharge from rainfall is low in dissolved minerals therefore large solutional channels and quick through flow times result in low concentrations of dissolved minerals (Worthington and Ford 2009).

While there was a gradient of electrical conductivity from limestone to sandstone to chalk geologies some minerals were characteristic of individual sites. Calcium was positively related to the chalk catchments particularly at 50cm depth. Circumneutral to alkaline pH was found across all river catchments studied and is indicative of the presence of reactive carbonate minerals in the geology at all river catchments (i.e. calcite, dolomite) (Kimblin 1995, Worthington and Ford 2009, Howden et al. 2010). Calcium is a major constituent of many carbonate minerals, and is derived from the shells of marine organisms which are the major component of calcite, aragonite, dolomite and ankerite which are all associated with sedimentary deposits. The highest levels of calcium in this study occurred in the hyporheic zone of the River Piddle. Calcium levels in chalk sediments can quickly reach saturation point with respect to calcite due to rapid kinetics in the fine grained chalk matrix (Shand et al. 2007). Levels of calcium were lower in the Frome than the Piddle catchment. The chalk layers of the Frome are overlain with Upper Greensand and Gault Clay (Tertiary deposits) (Adams et al. 2003, Howden et al. 2010) and as Tertiary deposits are slightly acidic decalcification will occur (Casey and Newton 1973). The Permo-Triassic sandstone sites had the lowest levels of calcium, partly due to the lower pH and partly because calcium in sandstone comes from dolomite which is less reactive than calcite and quickly becomes supersaturated (Shand et al. 2007) Calcium levels at the sandstone sites are sufficiently high not to influence the distribution and abundance of Crustacea at the sites (Capelli and

Magnuson 1983, Zehmer et al. 2002) reflecting the influence of the Keuper Marl layer on the local geology (Kimblin 1995).

Chloride was positively related to sites on the River Tone. Permo-Triassic sandstone aquifers can have high concentrations of chloride in groundwater from the overlying Quaternary glacial drift deposits (Mercia Mudstone) (Kimblin 1995). The Mercia Mudstone Group contains sandstone beds and evaporite minerals, mainly halite (sodium chloride) which is the source of the chloride in this study (Hobbs 2002). Mercia mudstone deposits result from sedimentary processes which occurred during the formation of Pangaea, during this period ancient seas dried up and left behind halite which is to this day affecting chloride levels in certain sandstone aquifers (Kimblin 1995). Chloride levels were also high in the unglaciated carboniferous limestone in comparison to the glaciated carboniferous limestone. This is explained by the presence of thermal waters in the Peak District region which are enriched in a number of solutes, particularly sulphate and chloride (Abessor and Smedley 2008).

The highest magnesium concentrations were found in the Permo-Triassic sandstone sites, in particular sites on the River Exe at 50cm and 20cm depth, magnesium concentrations were also strongly associated with sites in the Peak District. Magnesium is present in sedimentary rocks in the form of Dolomite and Calcite (Shand et al. 2007), and is at natural levels across all sites (Edmunds and Kinniburgh 1986). Calcite, which is abundant in chalk deposits contains lower levels of magnesium than dolomite, which is abundant in Permo-Triassic sandstone deposits, explaining the higher levels of magnesium occurring in the sandstone sites (Shand et al. 2007).

Electrical conductivity levels were high in the chalk streams and positively related to organic matter at 20cm depth and DO at 50cm depth during the summer and winter surveys. In the spring and summer months chalk streams have an abundant cover of macrophytes supplying large amounts of organic material to the system (Cotton et al. 2006) explaining the positive

relationship of organic matter (LOM) at 20cm depth. The positive relationship with DO at 50cm depth is unusual because many studies report the chalk to be clogged and degraded (Howden et al. 2010, Pulg et al. 2011). Previous studies have found chalk streams to have a thin biologically productive layer up to 20cm depth (Pretty et al. 2006) however, my sampling methodology (BOU-ROUCHE pumping) was not designed to examine fine scale changes in biological and chemical gradients.

In this study river catchments followed an electrical conductivity gradient related to hydrogeology and hydraulic conductivity across the geological types. Electrical conductivity levels were highest on the chalk geology and lowest on the limestone geology of the Yorkshire Dales. The pattern became less clear on the Devon sandstone and the limestone geologies of the Peak District where considerable site specific variability was observed. The influence of natural solutes on hyporheic water chemistry at the Peak District and sandstone geologies showed the influence groundwater geochemistry has the hyporheic zone of streams and rivers. These results highlight the importance of understanding the influence of regional groundwater chemistry on hyporheic and surfacewater chemistry when assessing streams and rivers (Pringle and Triska 2000)

Seasonal variability in hyporheic physicochemistry within river catchments: the role of hydrogeology

Seasonal patterns in hyporheic water chemistry are well studied (Findlay 1995, Wondzell 2011) and interactions between surfacewater and groundwater in the hyporheic zone vary seasonally. My second hypothesis was partly proven: i.e. in the hyporheic zone dissolved minerals will decrease and dissolved oxygen increase during winter supporting existing studies in this area (Fraser and Williams 1998, Navrátil et al. 2010). Where seasonal patterns were not apparent was in the chalk river catchments with dissolved ions increasing or at similar levels during both the summer and winter surveys. The strongest temporal pattern observed was the increase in DO concentrations during winter across seven out of eight river

catchments (except the Dove in the Peak District). Increased levels of DO related to high discharge and are well documented in the hyporheic zone, increased water pressure from swollen rivers force oxygen rich surfacewater into river bed sediments (Malard and Hervant 1999, Malcolm et al. 2004).

A decrease in electrical conductivity levels and groundwater associated ion concentrations across six out of eight river catchments (except the two chalk rivers) also supports a greater influence of surfacewater in the hyporheic zone during winter months, with groundwater influence more important during summer baseflow (Neal 2002). In a study on the River Thames at Wallingford, Darling and Talbot (2003) found isotopic enrichment of $\delta^{18}\text{O}$ (oxygen) and δD (deuterium) in surfacewater during summer months (heavier isotopes are an indicator of water not exposed to evaporation, e.g. groundwater). During October and November as rainfall increased the isotopic composition of $\delta^{18}\text{O}$ and δD in the surfacewater of the River Thames was depleted (i.e. rainfall subject to evaporative processes and is isotopically lighter in the heavier $\delta^{18}\text{O}$ and δD than groundwater) (Darling and Talbot 2003).

The two Chalk Rivers followed a different pattern to the other rivers in this study. In the Frome, groundwater associated ions had higher concentrations during the winter than during the summer surveys. Also the ion concentrations in the Piddle catchment were similar between seasons with magnesium higher during the winter. This is an unusual pattern as winter rainfall usually results in a dilution of ion concentrations in surfacewater and hyporheic water (Soulsby et al. 2007, Soulsby et al. 2009). Results from this study suggest groundwater influence on chalk hyporheic water chemistry is strong in both summer and winter. Groundwater influence on chalk streams is well documented (Darling and Talbot 2003) with groundwater discharge from Chalk aquifers providing a stable flow regime through the year. At 50cm depth groundwater flow patterns appear dominant in chalk streams throughout the year with surfacewater possibly penetrating into the upper sediment

layers. In a study on the River Lambourne, a chalk stream in southern England, groundwater inputs dominated at depths greater than 0.5m. At shallower depths the hyporheic zone was more dynamic though mixing was variable and inconsistent supporting results in this study (Lapworth et al. 2009, Allen et al. 2010)..

Groundwater-surfacewater interactions in the hyporheic zone: the influence of hydrogeology

The scale of groundwater-surfacewater interactions in the hyporheic zone is driven by the local geology and subsequently hyporheic sediment composition (Pepin and Hauer 2002, Olsen and Townsend 2003). Hydraulic conductivity is an important factor in governing dissolution rates of rocks and soils while also influencing the replenishment and uptake of key biogeochemical properties (DO, nutrients and minerals) in the hyporheic zone. My third hypothesis that coarse alluvial sediments will result in dynamic hyporheic zones with strong riffle-tail patterns was broadly proven. Strong vertical hydraulic gradients were observed in the two limestone catchments (coarse sediments) and weak patterns observed in the chalk catchments (fine sediments). Numerous studies describe downwelling water at the head of riffles and upwelling water at the tail of riffles (Marmonier 1986, Boulton et al. 1998, Marmonier et al. 2010) with the degree of hyporheic exchange through riffle features increasing with steeper hydraulic head gradients and coarser streambed sediments (Kasahara and Hill 2006).

The chalk geology is unique and has properties inconsistent with more dynamic systems where extensive vertical mixing of groundwater and surfacewater occurs (i.e. limestone sediments). Similar studies on the chalk hyporheic zone in the UK have shown weak vertical hydraulic gradient patterns (Davy-Bowker et al. 2006, Pretty et al. 2006) with a dominance of upwelling groundwater in the chalk hyporheic (Pretty et al. 2006). Chalk streams dependence on groundwater flow make them a truly groundwater dependent ecosystem

(Boulton and Hancock 2006) particularly at the reach or riffle scale. At larger scales patterns of losing and gaining are a common feature of chalk streams and have been studied extensively on the Frome and Piddle, with substantial surface water losses associated with the Broadstone Sand Formation and substantial groundwater inputs on the Greensand/Chalk and Palaeogene/Chalk Formations (Arnott 2009). Scale appears particularly important when studying the Chalk streams with vertical mixing of groundwater and surfacewater occurring at large scales (i.e. losing/gaining sections) with vertical mixing at small scales (i.e. bedform features) not observed at the depths studied in this project.

Longitudinal and vertical patterns in physicochemistry in riffle habitats: the influence of hydrogeology

Longitudinal patterns: head and tail of riffles

Patterns of water flow through riffle habitats often describe a downwelling zone at the head of the riffle and an upwelling zone at the tail of the riffle (Franken et al. 2001, Boulton 2007, Marmonier et al. 2010). This pattern of water flow gives rise to distinct physicochemical patterns at the head of the riffle (i.e. downwelling water rich in dissolved oxygen and low in electrical conductivity) and the tail of the riffle (i.e. upwelling water low in dissolved oxygen and electrical conductivity high). In this study dynamic up- and downwelling patterns were observed across the limestone and sandstone geologies with no patterns observed on the chalk geology which was dominated by upwelling groundwater. My fourth hypothesis (physicochemical differences between the head and tail of riffles will be greater at riffles with dynamic up- and downwelling zones) was not proven. Patterns across seven out of eight river catchments were inconsistent with only the Exe river catchment supporting evidence from the literature. At the Exe river catchment groundwater associated ions and electrical conductivity were higher in the tail of the riffle (upwelling zone) during both summer and winter surveys. The Exe hyporheic zone also had a high proportion of coarse sediments

suggesting that distinct physicochemical patterns may only occur at the head and tail of riffles containing a high proportion of coarse material.

Few studies have examined the hyporheic zone of the Exe catchment though it has been extensively studied regarding fine suspended sediment composition (Phillips and Walling 1999, Harlow et al. 2006). Studies on flow patterns through riffles on Permo-Triassic sandstone indicate high connectivity between surfacewater and groundwater in the hyporheic zone (Hannah et al. 2009) supporting results from this study. Pump times of water in the sandstone hyporheic were also low indicating high hydraulic conductivity in the sediment layers. The interaction in this study between a high proportion of coarse sediment and high hydraulic conductivities in the hyporheic zone of the Exe catchment may explain why textbook patterns of up- and downwelling occurred.

Across the other river catchments there was no pattern in physicochemistry between the head and tail of riffles. Dissolved oxygen was similar across all river catchments at the head and tail of riffles, a result consistent with other studies (Fowler and Scarsbrook 2002) suggesting mixing between surfacewater and groundwater is occurring throughout the riffle dampening any differences that may occur between hyporheic flowpaths through the head and tail of riffles.

Vertical patterns: depth

My fifth hypothesis (the influence of surfacewater physicochemistry will decrease with depth, whereas the influence of groundwater chemistry will increase with depth) was broadly proven. The hyporheic zone is often characterised by steep chemical gradients between mixing surfacewater and groundwater both vertically and laterally (Gibert et al. 1990, White 1993, Boulton et al. 1998, Williams et al. 2010). In particular, DO concentrations and pH decrease with increased residence time in the hyporheic zone greatly influencing the distribution of the hyporheos (Bencala 2000, Williams et al. 2010). Conversely, upwelling

groundwater is often rich in dissolved minerals and nutrients and also provides a relatively stable flow regime often rich in hypogean fauna (Malard et al. 2003a, Marmonier et al. 2010).

In this study pH and DO concentrations were significantly lower at 50cm than 20cm depth in seven out of eight river catchments (except the Frome). The results from this study broadly support similar studies examining mixing between surfacewater and groundwater (Vervier et al. 1992, Valett et al. 1997, Williams et al. 2010). When mixing is reduced or upwelling groundwater dominates (i.e. Chalk hyporheic) then the influence of downwelling surfacewater is reduced and consequently chemical gradients will be small or non-existent. Vertical gradients may exist in the chalk sediments but would not be detected by my sampling methods (BOU-ROUCHE pump). The high levels of DO at 50cm depth in the hyporheic zone of the Frome was unusual, also vertical hydraulic gradients were weak or positive in the Frome suggesting that DO levels at 50cm are being replenished from upwelling groundwater or karstic features. Karst type behaviour is a feature of Chalk with rapid groundwater flow associated with areas of Palaeogene cover (i.e. Frome catchment) and valley bottoms (MacDonald et al. 1998). Similarly, highly transmissive solutional channels are also present in the Chalk aquifer of the Thames catchment in southern England (Waters and Banks 1997).

Groundwater associated ion concentration showed considerable variability between and within catchments. Calcium was the only ion to show a consistent pattern of differences with depth across catchments. Calcium increased with depth at the Frome, Piddle, Tone and Derwent catchments and decreased with depth at the Dove catchment. A high calcium concentration at depth implies an increasing influence of groundwater with depth (Shand et al. 2007) and is a pattern found in other studies (Soulsby et al. 2001). Interestingly the River Frome was the only catchment where all groundwater associated ions (except sodium)

increased significantly as depth increased again indicating a dominance of groundwater in the chalk hyporheic zone and shallow mixing layer.

Conclusion

Hydrogeology and importantly sediment size exerts considerable influence on processes occurring in the hyporheic zone, in particular physicochemical and hydrological processes which influence qualitative and quantitative distribution of hyporheic (Bencala 1993) and benthic fauna (Malcolm et al. 2004). My results show how geology and associated sediment composition influence processes at the reach scale with hydrogeological properties attenuating connectivity between surfacewater and groundwater (i.e. chalk – high attenuation properties across short spatial scales; limestone – low attenuation properties across short spatial scales). Inputs of fine silts (colmation) to riverbed sediments can potentially disconnect these surfacewater and groundwater mixing processes (Boulton 2007). Results from this study can better inform management of rivers, in particular streams vulnerable to colmation (i.e. fine sediments attract more fine sediment whereas coarse sediments can self-clean through flushing (Nowinski et al. 2011). This has been shown in practice with the success of rehabilitated salmonid spawning sites increasing when the proportion of fine sediments is reduced (Dirksmeyer and Brunotte 2009). Potentially the conservation of impacted rivers with a high proportion of fine sediments may not be cost effective unless the input of fine sediments can be tackled and vertical connectivity restored.

Characteristic patterns of up- and downwelling described in the literature were observed in the majority of river catchments in this study (apart from chalk streams). Departures from the literature were also found with no patterns in physicochemistry observed at the head and tail of riffles. Only the Exe river catchment followed the classic description of Marmonier (1986) with electrical conductivity and groundwater ion concentrations higher at the tail than the head of riffles. In this study it was evident that vertical profiles existed with pH and DO decreasing with depth but longitudinal profiles were uncommon. Application of general

theories regarding water flow through riffle features was inaccurate; results suggest that hyporheic water is well mixed at both the head and tail of riffles with no differences observed except the Exe catchment where patterns were evident during both summer and winter surveys indicating a strong longitudinal profile.

Chapter IV: Local and Regional scale distribution of fauna in the hyporheos: Influence of hydrogeology, depth, physicochemistry and glacial history.

Abstract

Processes in the hyporheic zone are affected by sediment properties (e.g. size, shape) which are a product of the dominant local geology within a catchment. The hyporheic zone is a habitat for a variety of organisms (i.e. the hyporheos), a refuge for fauna from perturbations (e.g. floods, drought) and predation and migratory route for subterranean fauna. Research has shown sediment composition influences species assemblages (e.g. Copepoda abundant in gravelly substrates) and water chemistry (e.g. oxygen reduction) in the hyporheic zone. The hyporheic zone is a constituent part of stream ecosystems though at present regional scale patterns and controls on the distribution of the hyporheos are poorly understood. In this study I sampled the hyporheic zone (20 and 50cm depth) of eight UK river catchments that exhibit a range of sediment properties (i.e. high proportion of: fine (chalk) – mixed (sandstone) – coarse (limestone) sediment). Limestone river catchments were sampled north (Yorkshire Dales) and south (Peak district) of the southern extent of the Devensian glacial limit. River catchments were sampled during summer and winter. Fauna collected were identified and body size measured. Only one stygobite fauna (Syncarida: Crustacea (size 2-4mm)) was collected from north of the Devensian glacial limit. No large stygobite fauna (Niphargidae, Crangonyctidae 5mm)) were collected from limestone sites north and south of the Devensian. Niphargidae and Crangonyctidae were collected from chalk and sandstone geologies in the south of the UK. Species richness and abundance were highest in limestone catchments at both depths and seasons. Vertical patterns in species distribution were strong in the chalk river catchments (fine sediment) but were less apparent in limestone catchments (coarse sediment). No differences were found in species richness and abundance between the head and tail of riffles from all catchments during both seasons. Macrofauna body size was also lower at 50cm than 20cm depth in the chalk hyporheic with patterns weak across other geologies. The size distribution and abundance of the community at 20cm depth in coarse sediment river catchments indicated that large fauna were more abundant in the hyporheic zone of those catchments. The size distribution and abundance of the community at 50cm depth during both seasons indicated a decrease in abundance of large fauna. Stygobite species in the north of the UK appear to be rare or absent following extirpation during the Devensian glaciation with recolonisation slow or pathways fragmented. These results show that increased interstitial space positively influences species richness, abundance and body size of the hyporheos, highlighting the importance of protecting subterranean biodiversity, particularly from the ecological impacts of fine sediment inputs into our streams and rivers which will reduce both species richness and abundance of fauna.

Introduction

The hyporheic zone provides a habitat for many meio- and macrofaunal invertebrate assemblages (Meiofauna retained on 63µm sieve and pass through a 500 µm sieve - macrofauna retained on 500 µm sieve) (Orghidan 1959, Stanford and Gaufin 1974, Williams and Hynes 1974, Hynes 1983). The community composition of hyporheic assemblages has been extensively studied in Europe (Danielopol 1989, Dole-Olivier et al. 2009b), Australia (Marchant 1995, Boulton et al. 2003b, Byrne et al. 2008) and North America (Strayer et al. 1993, Hunt and Stanley 2003, Varricchione et al. 2005) although few studies rarely extend beyond the reach scale (Hunt and Stanley 2003). Recently, a major European study (PASCALIS) examined geographic patterns of groundwater and hyporheic fauna and highlighted the uniqueness of subterranean habitats and also importantly our lack of knowledge of these habitats (PASCALIS 2002, Deharveng et al. 2009).

The PASCALIS project collected a total of 380 species and subspecies from 40 different families with 70% of the fauna collected endemic to France and 156 out of a total of 380 species collected from a single 400km² area (Ferreira et al. 2007). Endemism is high in subterranean waters primarily due to habitat fragmentation (Gibert and Deharveng 2002), also migration through subsurface environments is slow and hindered by geomorphic and hydrogeological barriers (Ward and Palmer 1994). Consequently, extirpation of fauna by glacial events can severely impact stygobite fauna with recolonisation post glaciation (i.e. to higher latitudes/altitudes) occurring at temporal scales of up to 10⁻³ years (Galassi et al. 2009b, Martin et al. 2009, Robertson et al. 2009, Stoch and Galassi 2010). In the UK the Devensian glaciation was our most recent glacial event (c. 18000 BP) covering Scotland and large parts of Northern England. At present UK stygobite records are concentrated in England and Wales with the frequency of species records increasing with increasing distance south of the southern extent of the Devensian glacial limit (Knight 2008, Robertson et al. 2009).

While glaciation can influence the distribution of stygobite fauna regionally other factors are also important drivers of the regional distribution of hyporheic fauna (the hyporheos). Groundwater-surfacewater interactions in the hyporheic zone are strongly determined by catchment geology (i.e. alluvial hydrogeological properties) (Valett et al. 1997, Soulsby et al. 2007). Coarse grained hyporheic sediments are common on karst or granitic geologies with fine grained hyporheic sediments common on chalk or clay-like geologies (Morrice et al. 1997, Hiscock 2007). Sediment composition will influence physicochemical conditions in the hyporheic zone with coarse grained sediments characterised by high concentrations of dissolved oxygen (DO) and coarse particulate organic matter (CPOM) from surfacewater input. Whereas, fine sediments are often low in DO with CPOM attenuated with increasing distance into the fine sediments. Thus, sediment composition influences the size, morphology, tolerance and behaviour of epigean (Brunke and Gonser 1997, Dole-Olivier et al. 1997, Swan and Palmer 2000) and hypogean fauna in the hyporheic zone (Danielopol 1989, Mösslacher 1998) with community composition changing as sediment proportions change across different hydrogeological regions. Therefore the use of hydrogeological regions to describe hyporheic communities could be a valuable tool in the management and conservation of this habitat.

Geology is the dominant influence on sediment size across hydrogeological regions, although locally hyporheic sediment structure will contain a 3-dimensional mosaic of sediment patches of different sediment sizes and proportions (Naegeli et al. 1996). Regulation of aquatic processes and the distribution of epigean and hypogean species at riffle-pool scales are regulated by hydrological flowpaths i.e. up- and downwelling water (Olsen and Townsend 2003, Marmonier et al. 2010). The strength of up- and downwelling in the hyporheic zone is controlled locally by bed sediment composition and strength of hydraulic head between the riffle head and tail (Kasahara and Hill 2006). Movement of surfacewater (i.e. hydraulic conductivity) both vertically and longitudinally through riffle

features is controlled by the dominant local sediment composition with hydraulic conductivity increasing (higher flow rate) as sediment grain size increases (Sharp 1988). Characteristic features of water flow through riffle features include: downwelling surfacewater at the riffle head often rich in DO with dissolved minerals low in concentration, whereas upwelling water at the riffle tail is often low in DO and rich in dissolved minerals (Marmonier et al. 2010). Consequently, downwelling zones can be dominated by epigeal fauna, whereas hypogean fauna can dominate in upwelling zones (Marmonier 1986, Marmonier et al. 2010). These distributional patterns of hyporheic fauna in riffles are often described from sites with high connectivity and gravelly substrates (Franken et al. 2001, Pepin and Hauer 2002, Marmonier et al. 2010) with attempts to describe distribution patterns in riffles with low connectivity and fine sediment composition more elusive (Davy-Bowker et al. 2006).

Body size and growth are life history traits that vary temporally and spatially among and within populations and are strongly affected by environmental (abiotic and biotic) conditions (Indermaur et al. 2010) which affect population growth, abundance and distribution (Loehle 2006). In benthic sediments the invertebrate assemblage is often composed of relatively few large individuals (macrofauna) with small individuals (meiofauna) increasingly abundant in the sub-surface (Stead et al. 2004). Although, sharp decreases in the abundance of meio- and macrofauna have been observed in chalk streams (Tod and Schmid-Araya 2009) and meiofauna in fine carbonate sediments (Beier and Traunspurger 2003). Coarse sediments are larger than fine sediments therefore interstitial space is larger allowing colonisation by a large variety of fauna of different sizes and morphology (shape). Body morphology is an important factor controlling colonisation in the hyporheic zone with riverbed sediments described as a distance filter (Wright et al. 1997) with good dispersers (i.e. meiofauna - small body size) found in high abundance in the hyporheic zone with bad dispersers (i.e. macrofauna – large body size) low in abundance (Omesova et al. 2008). In mountain

streams, macroinvertebrate fauna have long been known to thrive in deeper sediment layers (Stanford and Gaufin 1974, Williams and Hynes 1974) although in the hyporheic zone of streams containing a high proportion of fine sediment, sharp reductions in abundance of macrofauna has been observed (Weigelhofer and Waringer 2003a, Navel et al. 2010b). Reasons for movement vertically of macrofauna into the hyporheic zone can be to reduce intra- and inter-taxon specific competition with vertical migration also occurring in response to disturbance events (i.e. floods, droughts) (Palmer et al. 1992). Accessibility of hyporheic sediments for both meio- and macrofauna could be a useful tool in future management methods, particularly in response to predicted UK climate change scenarios (i.e. increase in winter floods and summer droughts) (UKWIR 2002) with hydrogeological areas associated with fine sediment composition particularly vulnerable.

The high endemicity of fauna in groundwaters and the hyporheic zone in many regions of the world highlights the need for greater knowledge of the hyporheic zone particularly in poorly studied areas such as the UK. Currently, the majority of hyporheic research in the UK has been at the reach scale (Stead et al. 2004, Wood et al. 2005, Schmid and Schmid-Araya 2010, Wood et al. 2010) with a few regional scale studies undertaken, notably Rundle and Ramsay (1997) who examined microcrustacean communities in upland and lowland habitats. A regional scale study was recently undertaken examining the hyporheos of alluvial gravels in Scottish rivers (Pryce et al. 2010) with the Scottish hyporheos containing no stygobite fauna consistent with results from other studies on areas affected by Quaternary glaciations (Strayer et al. 1993, Varricchione et al. 2005, Robertson et al. 2009). UK regional scale patterns of hyporheic assemblages are poorly described and understood with the majority of reach scale studies conducted in the south of England (Wood et al. 2012). In the UK a diverse range of geological types exists exhibiting a range of physical and chemical characteristics which potentially harbor rich and diverse hyporheic communities. In particular, the geological and glacial history of the UK is unique in Europe and provides an

excellent study site to examine patterns and controls influencing hyporheic communities. This study examines different hydrogeological regions and associated regional scale patterns of physicochemistry and subsequent influence on the species richness, abundance and body size of hyporheic communities. The following hypotheses are tested:

- (1) Distribution of stygobite fauna will be influenced by the southern extent of the Devensian glaciation. Stygobite fauna (i.e. Niphargidae, Crangonyctidae) will be more abundant south of the Devensian glacial limit with species absent or rare north of the glacial limit.
- (2) Meio- and macroinvertebrate species richness and abundance in the hyporheic zone (20cm and 50cm depths) will increase as geology becomes increasingly resistant to weathering and the proportion of coarse sediment increases. Patterns will be tested during both winter and summer to also see if seasonality influences the spatial distribution of fauna in the hyporheic zone.
- (3) In riffle habitats the distribution of epigeal and hypogean meio- and macroinvertebrate assemblages will differ between riffle heads and tails (longitudinally) and also vertically (20cm and 50cm depths). Longitudinal and vertical differences in abundance will be amplified as the proportion of fine sediment increases (i.e. decreasing hydraulic conductivity). Differences will be tested during both winter and summer to see if seasonality influences the spatial distribution of fauna in the hyporheic zone.
- (4) Reach scale vertical patterns (20 - 50cm depth) in the body morphology (size) of fauna will be most apparent in river catchments with fine sediment composition as penetration of the sediment interstices by larger fauna is restricted.

(5) Regional scale patterns in the body size – abundance community size distribution will vary according to sediment size resulting in a shallower slope for river catchments with a high proportion of coarse sediments (i.e. large bodied fauna abundant in the hyporheic zone) and steeper slope at river catchments with a high proportion of fine sediments (i.e. large bodied fauna low in abundance in the hyporheic zone). The steepness of slopes will increase with increasing depth (i.e. 20cm to 50cm) with a reduction of large bodied fauna. Similarly the slopes at 50cm depth will increase in steepness from summer to winter when the hyporheic community is dominated by early instar invertebrate larvae.

Methods

Study site

The sample sites were located on geologies with characteristic hydrogeological properties influencing the sediment composition in the hyporheic zone. The geologies chosen for this study were Carboniferous limestone (coarse gravelly substrate), Permo-Triassic sandstone (coarse sand substrate), Cretaceous Chalk (fine chalk substrate). An extra Carboniferous limestone site was selected to have comparable sites north and south of the southern extent of the Devensian glacial limit (See Chapter 2 for detailed site descriptions).

Sampling was undertaken during summer (June/July 2008) and winter (October/November 2008). At each geological region (chalk, sandstone and two limestone areas) two river catchments were selected with good chemical and biological water quality and four riffle habitats chosen from each river catchment. During the summer survey hyporheic samples were collected from the head and tail of each riffle at depths of 20cm and 50cm (three replicate samples taken from each depth). During the winter survey the preceding method was used though samples were only taken from 50cm depth. The glacial effect survey on the two limestone catchments also followed the preceding methods.

Glacial influence survey (Summer): 4 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 2 depth = 192 samples.

Glacial influence survey (Winter): 4 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 1 depth = 96 samples.

Summer sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 2 depths = 384 samples.

Winter sampling survey: 8 catchments x 4 riffles x (3 upwelling + 3 downwelling) x 1 depth = 192 samples.

Piezometers were hammered into the riverbed using a sledgehammer (20cm and 50cm depths) at the head and tail of each riffle. Piezometers were spread laterally across the head and tail of each riffle and spaced at least 1m apart and always more than 2 metres from the river bank. The riffle tail was sampled first followed by the riffle head to minimise disturbance. A volume of five litres of hyporheic water was extracted using the BOU-ROUCH pump and filtered through a 63µm mesh sieve. The collected sample was preserved in 70% industrial methylated spirits for later sorting and identification of fauna and sediment. Invertebrates collected in each sample were identified to the lowest taxonomic level possible and body size of each individual measured (See chapter 2 for detailed sampling methods).

Dissolved oxygen, electrical conductivity, pH and temperature were measured directly from the piezometer using portable field meters. Water samples were extracted from the piezometer and frozen on day of collection for laboratory analysis of cations and anions. Vertical hydraulic gradients (VHG) were measured at the head and tail of each riffle to determine the degree of up- and downwelling. Pump times were measured for each 5 litre sample to give an indication of the sediment composition at 50cm depth. Sediment samples

were collected from a depth of 20cm and sorted into size fractions (phi scale -4 to 4) in the laboratory (see Chapter 2 for detailed description of methods).

Statistical analysis

Ordinations

The datasets for the analysis of the species-environment relationships were broken down into separate depths and the subsequent analysis of each depth dataset conducted at high and low groundwater levels. The species-environment relationship of all species were initially analysed on the basis of presence-absence relationships to give all species including rare species equal weights. Subsequent analysis was undertaken with rare species removed from the dataset and species scores then weighted by including abundance data. Initially detrended correspondence analysis was undertaken on the species-environment datasets to ascertain a linear or unimodal response curve, if the compositional gradient length is greater than 2 SD units (Hill and Gauch 1980) suggesting a unimodal species response curves then CCA is the appropriate method. If the species response curve was unimodal then canonical correspondence analysis was undertaken to study the relationships between the species and physicochemical dataset (ter Braak 1987).

Water chemistry data were $\log_{10}(n+1)$ transformed where appropriate if data were skewed to normalise the data distribution. Species abundances were $\log_{10}(n+1)$ transformed to reduce the effect of dominant taxa in the dataset. Each geological area in each region was assigned a score from 1 to 4 following the methods described in Stoch et al (2004). This score increased with increasing permeability, hydraulic conductivity and decreased conductivity (SEC) using information collected during the sampling campaign. The scores include 1 (cretaceous chalk aquifer: high SEC, low hydraulic conductivity); 2 (permo-triassic sandstone aquifer: high SEC, med-high hydraulic conductivity); 3 (Karst aquifer: medium-low SEC, high hydraulic conductivity,); 4; (Karst aquifer; low SEC, high hydraulic conductivity). Forward selection

of the environmental variables was conducted to ascertain the main drivers of community composition for 20 and 50cm depth at low groundwater and at 50cm depth at high groundwater and the presence-absence dataset.

The statistical significance of each environmental variable was tested using forward selection and performed using a Monte–Carlo permutation test (999 random permutations) with the environmental variables retained for the pCCA having a significance level of $P \leq 0.05$ (ter Braak and Schaffers 2004). The distribution of sites and associated species within geological areas with respect to the calculated pCCA axes is summarised using confidence ellipses (two standard deviations). Each confidence ellipse is centered at the mean value of the population and represents a 95% CI of that mean. All statistical analyses were performed with R version 2.11.12 (R Development Team, 2010). Ordinations were performed with the “vegan” package version 1.8-3 (Oksanen et al. 2006). Confidence ellipses were calculated using the “ellipse” package version 0.3-5 (Murdoch and Chow 2007).

Generalised linear model

Generalised Linear models allow the distribution of the response variable to be fitted correctly whether the distribution follows a Gaussian, Poisson, negative binomial, geometric or gamma distribution (Zuur et al. 2009). To accommodate for under- or over-dispersed poisson data quasi-poisson errors were fitted to the model (Wedderburn 1974). Under or over dispersion occurs when the residual deviance is much greater or much less than the residual degrees of freedom. The use of quasi-poisson errors allows the dispersion parameter to be estimated rather than using the default value of 1 set in a Poisson distribution. Stepwise model selection was performed for each species and higher taxa. The full model with all interactions was reduced in a stepwise manner. The reduced model was compared to the full model using an analysis of deviance test, the optimal model is reached when the model comparison becomes significant indicating no further reduction is possible and the optimum

model has been reached. For the analysis, riffle, depth and up/downwelling were treated as fixed factors. The use of riffle as a random factor was not possible due to the use of quasi-likelihood methods in mixed models at the edge of statistical design (Zuur et al. 2009).

Differences in body size were evaluated using ANCOVA, a multiple regression-based method. As mentioned previously GLM models allow the response variable to be fitted correctly, the response variable (body size) is continuous. Similarly all body size measurements are positive with no zero values allowing a gamma or gaussian distribution to be fitted to the data. Homogeneity of the regression slopes was tested if the difference between slopes is not significant then the model is valid and the ANCOVA can proceed. Backward elimination of statistically non-significant factors was employed to obtain the optimum model. The community size spectrum was calculated by logarithmic binning of the abundance of all body sizes (M) measured (meio- and macroinvertebrates) from each river catchment at two depths (20 and 50cm) and two seasons (winter and summer). The range of body sizes (M) was divided into 10 size bins of equal length and regressed against the bin centres (White et al. 2008) Post-hoc tests were performed using the package “Multcomp” version 1.2-5 (Bretz et al. 2010). All statistical analyses were performed with R version 2.11.12 (R Development Core Team 2010).

Table 4:1. Nested linear mixed effects model comparing species richness across geological areas.

<i>Comparison</i>	<i>df</i>	<i>F</i>	<i>P</i>
Summer 20cm	1,160	50.45198	<0.001
Summer 50cm	1,160	31.39721	<0.001
Winter 50cm	1,160	19.37366	<0.001

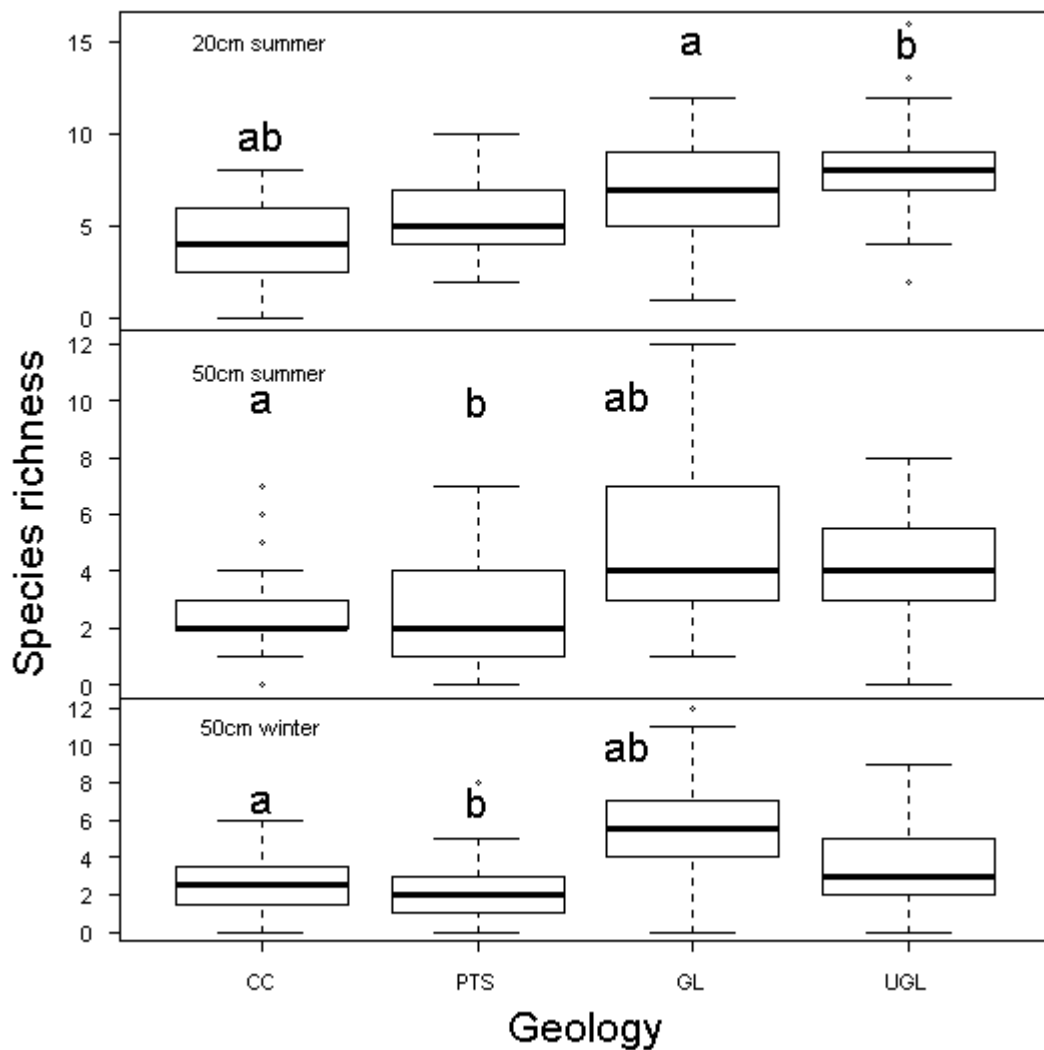


Figure 4:1. Boxplots showing species richness observed in the hyporheic zone (20cm and 50cm depth) at each hydrogeological area during summer and winter. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified Boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Letters that are the same indicate a statistically significant difference ($p < 0.01$). Key: CC = chalk, PTS = sandstone, GL = glaciated limestone, UGL = unglaciated limestone.

Results

Species richness and abundance of the hyporheos across hydrogeological regions

A total of 77 species and higher taxa were collected during the study from the summer and winter sampling surveys (Appendix 2 & 3). Dominant taxa ubiquitous across all river catchments included: Oligochaeta, Chironomidae, Nematoda, Acari, Glossosomatidae,

Limnius sp. and *Baetis* sp. and all collected from both 20cm and 50cm depths during the summer and winter sampling surveys. During the summer survey at 20cm depth species richness was highest across the limestone sites (Ure, n = 32; Wharfe, n = 33; Dove, n = 34; Derwent, n = 35). Species richness was lower at both sandstone river catchments (Exe, n = 30 and Tone, n = 25) (Appendix 2). Both chalk catchments had the lowest species richness at 20cm depth (Frome, n = 23 and Piddle, n = 18) (Appendix 2). Species richness was significantly higher in the limestone catchments in comparison to the chalk catchments at 20cm depth during the summer survey (Table 4.1, Fig. 4.1). At 50cm depth species richness was also higher in the limestone catchments in comparison to the chalk and sandstone catchments though only significantly higher in the Yorkshire dales river catchments (Table 4.1, Fig. 4.1). During the winter sampling survey at 50cm depth species richness was also highest at the limestone catchments (Wharfe and Dove, n = 20) with the lowest species richness occurring at the Tone catchment (n = 8) and similar at the Frome, Ure and Derwent catchments (n = 16), Exe catchment (n = 15) and Piddle catchment (n = 14) (Appendix 3).

Stygobite fauna

Stygobite fauna were found in low abundances in the hyporheic zone with stygobite abundance dominated by the Niphargidae (Gammaridae: Amphipoda) family. Distribution of Niphargidae was restricted to sites in Dorset (Frome and Piddle) and Somerset (Tone) (Appendix 2). During the summer sampling survey stygobites were dominated by three species of the family Niphargidae: *Niphargus aquilex*, *N. fontanus* and *N. kochianus* all collected from sites located south of the southern extent of the Devensian glacial limit. The most abundant Niphargidae collected in this survey was *N. aquilex* with specimens collected at both chalk streams, from the Piddle at both 20cm and 50cm depth and the Frome at 50cm depth. Niphargidae were also abundant at the Tone catchment located on the sandstone geology at 50cm depth. *N. aquilex* was also the only Niphargidae collected during the winter survey with specimens collected from both chalk streams (Frome and Piddle) at 50cm depth.

All other Niphargidae collected from the summer survey were located on the chalk streams with *N. fontanus* collected from the Frome at both 20cm and 50cm depth and the Piddle at 50cm depth, with *N. kochianus* collected from the Piddle at 50cm depth (Appendix 2). The stygobite amphipod *Crangonyx subterraneus* (Gammaridae: Amphipoda) was also only collected from chalk streams with specimens collected from the Frome at 50cm depth (Appendix 2). Only one stygobite species *Antrobathynella stammeri* (Bathynellacea: Syncarida) was collected from sites north and south of the Devensian glacial limit with specimens of *A. stammeri* collected from the Wharfe river catchment on the limestone geology at 50cm depth and from the Tone river catchment on the sandstone geology at both 20cm and 50cm depth (Appendix 2).

Stygophile fauna

Stygophile species were dominated by two orders of Copepoda (Harpacticoida and Cyclopoida). Harpacticoida collected during the summer sampling survey were dominated by the family Canthocamptidae with three species dominant: *Bryocamptus zschokkei*, *B. minutus* and *B. echinatus* and collected from all river catchments with abundance high on the limestone geologies of the Yorkshire Dales and the Peak District (Appendix 2). Other Canthocamptidae collected included *Bryocamptus pygmaeus* collected from the limestone river catchment of the Dove, Derwent and Ure from both 20cm and 50cm and from the Piddle river catchment located on the chalk from 50cm depth and *Bryocamptus weberi* collected from the Ure and Wharfe limestone river catchments from 20cm and 50cm depth (Appendix 2). Members of the family Canthocamptidae collected in lower abundance included *Attheyella crassa* collected from all river catchments except the Piddle located on the chalk. Importantly, *A. crassa* was only found at both 20cm and 50cm depths across the limestone catchments with distribution inconsistent in the chalk and sandstone hyporheic. Specimens of *A. crassa* were also collected from the Exe catchment (sandstone) at 20cm depth and the Frome (chalk) and Tone (sandstone) catchments at 50cm depth (Appendix 2 &

3). Two other *Attheyella* sp. were also collected though in low abundances and found exclusively in the northern limestone sites at 20cm depth: *Attheyella bidens* and *A. trispinosa*. One notable Harpacticoida species collected was *Nitokra psammophila* (Family: Ameiridae) with an extremely limited distribution with specimens only collected from the Exe catchment (sandstone) during both seasons with abundance high at 20cm depth and reduced at 50cm depth (Appendix 2).

During the winter sampling survey *B. zschokkei*, *B. minutus* and *B. echinatus* were again the dominant Harpacticoida collected with abundance high across all limestone river catchments (Appendix 3). Notably, only *B. minutus* and *B. pygmaeus* were collected from the chalk streams with abundance low. No *Bryocamptus* sp. were collected from either sandstone river catchment. Other notable Harpacticoida collected included *Attheyella* sp. (Canthocamptidae) collected from the Frome, Piddle and Derwent river catchments with abundance low in comparison to the summer survey. *Nitokra psammophila* (Ameiridae) was again also collected in high abundance from the Exe catchment (sandstone) (Appendix 3).

During the summer survey Cyclopoida were dominated by *Diacyclops* sp. (Cyclopidae) and *Acanthocyclops* sp. (Cyclopidae) and abundant in both the sandstone and limestone river catchments (Appendix 2). No Cyclopoida were collected from the hyporheic zone of both chalk river catchments. Other notable Cyclopoida collected from the summer survey include *Paracyclops* sp. (Cyclopidae) collected from the Wharfe and Dove river catchments on the limestone at 20cm depth, and *Macrocyclus* sp. (Cyclopidae) collected at both 20cm and 50cm depth from the Dove river catchment (limestone) and the Exe river catchment (sandstone). *Paracyclops* sp. was also collected from the Wharfe and Dove river catchments on the limestone at 20cm depth and at 50cm depth from the limestone river catchments of the Ure, Wharfe and Dove (Appendix 2). During the winter sampling survey Cyclopoida were again dominated by *Acanthocyclops* sp. and *Diacyclops* sp. with *Acanthocyclops* sp.

collected from all catchments except the two chalk streams (Frome and Piddle) and *Diacyclops* sp. collected from all catchments except the Frome chalk stream (Appendix 3).

Stygoxene fauna

Members of the Orders Ephemeroptera, Plecoptera, Trichoptera and Elmidae were common at both 20cm and 50cm depths during the summer survey with abundance reduced during the winter survey. Many members of the previously mentioned groups can be termed both stygophile and stygoxene with early and later instars exploiting the hyporheic zone during their life cycle. Taxa found consistently at both 20cm and 50cm depths included: *Leuctra* sp., *Ephemerella* sp., *Baetis* sp., *Glossosoma* sp., *Agapetus* sp., *Esolus* sp. and *Limnius* sp. (Appendix 2 & 3).

During the summer sampling survey late instar *Leuctra* sp. were only collected from 50cm depth in the limestone river catchments of the Ure, Wharfe, Dove and Derwent, whereas early instar *Leuctra* sp. were collected from the majority of river catchments (except the Exe (sandstone) and Derwent (limestone)) from 50cm depth (Appendix 2). During the winter survey the late instar *L. hippopus* was only collected from the Wharfe and Dove river catchments on the limestone. Early instar *Leuctra* sp. were only collected from the Exe (sandstone) and Dove (limestone) river catchments (Appendix 3).

During the summer survey two members of the order Ephemeroptera (*Baetis* sp. and *Ephemerella* sp.) were common across all geologies. *Baetis* sp. were collected at all catchments except the Dove (limestone) at 20cm depth and at all catchments except the Frome (chalk) at 50cm depth. *Ephemerella* sp. were collected from all river catchments except the Tone (sandstone) at 20cm depth and from all catchments except the Frome (chalk), Tone (sandstone) and Wharfe (limestone) at 50cm depth (Appendix 2). In comparison *Caenis* sp. were only collected at 20cm and 50cm depth from the limestone river catchments (Appendix 2). During the winter survey *Baetis* sp. were only collected from the

Frome, Exe and Dove catchments with abundance reduced from the summer survey. As in the summer survey *Caenis* sp. were abundant on the limestone geologies of the Wharfe, Dove and Derwent river catchments, with specimens also collected in low abundance from both chalk streams (Frome and Piddle) (Appendix 3).

Two members of the Trichoptera family (*Glossosoma* sp. and *Agapetus* sp.) were collected from both 20cm and 50cm depths during the summer survey with *Glossosoma* sp. found consistently across all river catchments at 20cm and 50cm depths except the Tone catchment at 50cm (Appendix 2). *Agapetus* sp. were only collected at 50cm depth in the two chalk catchments (Frome and Piddle) and from all the river catchments except the Exe (sandstone and Ure (limestone) at 20cm depth (Appendix 2). During the winter survey *Glossosoma* sp. were collected across all river catchments except the Exe (sandstone) and Wharfe (limestone). *Agapetus* sp. were collected in high abundances from the two chalk streams (Frome and Piddle) and from the limestone catchments in the Peak district (Dove and Derwent) (Appendix 3).

Members of the Elmidae family varied in their regional distribution with juvenile *Limnius* sp. collected across all river catchments at both depths during the summer survey and all river catchments at 50cm depth during the winter survey (Appendix 2 & 3). Adult *Limnius* sp. were only collected from the Tone (sandstone) and Derwent (limestone) river catchments from 20cm depth. In comparison, juvenile *Esolus* sp. were collected from sandstone and limestone river catchments at both depths during the summer survey and winter survey at 50cm depth with no specimens collected from the two chalk streams (Frome and Piddle) (Appendix 2 & 3).

During the summer survey *Gammarus pulex* (Gammaridae: Amphipoda) was found across all river catchments except the Ure and Wharfe (limestone) in the Yorkshire Dales. Contrary to abundance patterns of many species *G. pulex* abundance at 20cm depth was highest at both chalk streams (Frome and Piddle) with abundance also high at the Derwent (limestone) and Tone (sandstone) river catchments. Interestingly, *G. pulex* was not collected from the hyporheic zone of both the Ure and Wharfe river catchments (limestone) in the Yorkshire Dales (Appendix 2). Other notable Crustacea collected included *Asellus aquaticus* (Crustacea: Isopoda) with abundance high at both 20 and 50cm depths at the limestone site on the River Manifold in the Peak District (Appendix 2). During the winter survey *G. pulex* abundance at 50cm depth was low with specimens collected from the Frome (chalk), Exe (sandstone) and Dove limestone) river catchments. During the winter survey no specimens of *A. aquaticus* were collected (Appendix 3).

The influence of the Devensian glaciation on the regional scale distribution of stygobites

Model 1 includes all species collected from the summer sampling survey (2008) and importantly all stygobite species. The ordination was calculated using binary (presence/absence) data to give equal weight to rare species (i.e. stygobite fauna). The results of the forward selection of the four pCCA models are shown in Table 4:2. The results for the summer survey including species presence/absence data (Model 1) identified eight significant variables: pH, chloride, calcium, sulphate, potassium, conductivity, geology and depth. Conductivity was removed from the model as it was highly negatively correlated with geology. The amount of variation explained by the chosen variables is 6.5%. The first variable selected was geology (eigenvalue = 0.195) explaining 19.2% of the variation of the constrained variables followed by calcium (eigenvalue = 0.118, 12%), sulphate (eigenvalue = 0.113, 11.1%) and pH (eigenvalue = 0.089, 8.8%). The first six axes chosen using Monte-Carlo permutation tests for Model V1a were highly significant ($p < 0.01$) the following two axes were significant ($p < 0.05$).

Table 4:2. Results from pCCA forward selection for both summer and winter sampling surveys from 20cm and 50cm depths. Model 1 results are for binary data (presence/absence), Model 2 = summer survey at 20cm depth, Model 3 = summer survey at 50cm depth, Model 4 = winter survey at 50cm depth. Number of taxa and total inertia for each analysis are given. Statistically significant variables selected during forward selection are indicated with associated significance value (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Model	1		2		3		4	
Number of taxa	68		57		28		32	
	Inertia	Proportion	Inertia	Proportion	Inertia	Proportion	Inertia	Proportion
Total	10.129	1.000	5.440	1.000	4.121	1.000	4.525	1.000
Constrained	0.663	0.065	0.340	0.062	0.224	0.055	0.391	0.080
Unconstrained	9.467	0.935	5.100	0.937	3.896	0.945	4.134	0.913
	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
pH	3.252	0.005**	1.714	0.035*	1.369	0.310	1.586	0.090
Cl	1.550	0.045*	2.227	0.005**	1.630	0.130	1.058	0.620
Ca	3.054	0.005**	1.414	0.150	2.710	0.010**	1.313	0.340
NO3	1.487	0.055	1.341	0.250	1.653	0.125	1.123	0.430
SO4	2.700	0.005**	1.314	0.320	3.394	0.005**	5.080	0.005**
K	1.909	0.015*	1.304	0.240	1.114	0.660	1.372	0.190
DO	1.087	0.23	1.268	0.300	1.399	0.370	1.417	0.250
cond	3.328	0.005**	2.746	0.005**	1.551	0.230	1.267	0.410
LOM	1.292	0.16	1.151	0.470	1.142	0.620	0.701	0.950
Na	1.536	0.055	1.117	0.420	1.478	0.300	0.883	0.850
Mg	1.425	0.075	0.997	0.750	0.801	0.910	2.399	0.005**
Geology	4.511	0.005**	3.687	0.005**	3.815	0.005**	3.790	0.005**
Depth	5.533	0.005**						

The only purely stygobitic crustacean found in sites north and south of the Devensian glacial limit was *Antrobathynella stammeri* (As) collected from the Tone (sandstone) and Wharfe (limestone) river catchments (Figure 4:2). All other stygobite fauna were collected from the chalk and sandstone geologies located in Dorset and Somerset, southern England. Calcium and depth were positively correlated with all *Niphargus* sp. (Figure 4:2; Appendix 2 & 3) in particular *Niphargus kochianus* (Nko) collected only from the Piddle river catchment on the chalk, with calcium concentrations relatively high in the hyporheic zone at 50cm depth. Two Niphargidae species (*Niphargus fontanus* (Nfo) and *N. kochianus* (Nko)) were also only collected from the hyporheic zones of the two chalk streams (Frome and Piddle). The distribution of *Niphargus aquilex* (Naq) was more extensive with specimens collected from the Tone river catchment on the sandstone geology in Somerset and also from both chalk streams (Frome and Piddle). The only other stygobitic Amphipod collected was *Crangonyx subterraneus* (Csu) and also collected only from the Frome river catchment on the chalk (Figure 4:2).

Regional scale distribution of the hyporheos across hydrogeological areas

Results from the summer survey at 20cm depth (Model 2) identified four significant variables: conductivity, geology, pH and chloride. The amount of variation explained by the significant variables is 6.25%. The first variable selected was electrical conductivity (eigenvalue = 0.150) explaining 44.2% of the variation of the constrained variables followed by geology (eigenvalue = 0.085, 25%), pH (eigenvalue = 0.064, 18.9%) and chloride (eigenvalue = 0.041, 12%). The first three axes of Model 2 were highly significant ($p < 0.01$) with axis 4 significant ($p < 0.05$). Model 2 includes abundant species collected from 20cm depth from the summer sampling survey (2008) with uncharacteristic outlying rare species identified in Model 1 removed from the analysis. The ordination was calculated using abundance data with weights related to abundance given to each species to remove compression of data in the centre of the ordination plot. Electrical conductivity (1st axis) and geology (2nd axis) explained the most variation within model 2 (Table 4.2, Fig. 4.3). Catchments with characteristically fine sediment composition were positively associated with electrical conductivity and conversely coarse sediments positively associated with geology (i.e. positive end of geology gradient (coarse grained sediment), negative end (fine grained sediment)).

Results from the summer sampling survey at 20cm depth showed many species positively correlated with geology and negatively correlated with electrical conductivity. Many species fell within the 95% confidence ellipses of the two limestone areas (Fig. 4.3). The two limestone areas had similar species assemblages; particularly many *Leuctra* spp. and Elmidae were abundant in the hyporheic zone at 20cm depth (Appendix 2). Harpacticoida were abundant across all limestone sites, in particular members of the family Canthocamptidae (*Bryocamptus zschokkei* (Bz), *B. minutus* (Bm) and *B. echinatus* (Be)). Two other *Bryocamptus* sp. were collected from the limestone areas with *B. pygmaeus* (Bp) abundant in the Peak District and *B. weberi* (Bw) abundant in the Yorkshire Dales, with

Attheyella crassa (Ac) (Canthocamptidae) also abundant across the limestone areas (Fig. 4:3). The Ure catchment in the Yorkshire Dales had a cluster of outlying species which were low in abundance elsewhere, for example the stoneflies *Isoperla* sp. and *Perlodidae* sp. and the adult riffle beetle *E. parallelepipedus*. Only a few species were characteristic of the chalk catchments at 20cm depth such as: (*Agapetus* sp. (Ag) (Glossosomatidae), *Limnius volckmari* (Lvj) (Elmidae), *Diura bicaudata* (Dbi) (Perlodidae) and *Gammarus pulex* (Gp) (Gammaridae) (Fig. 4:3). The two sandstone catchments had a similar species assemblage to the chalk catchments apart from *Canthocamptus staphylinus* (Cs) (Canthocamptidae) which was only collected from the sandstone catchments (Figure 4:3). Taxa ubiquitous across all river catchments and clustered around the centre of the ordination plot include: Chironomidae (ch), Oligochaeta (ol), *Dicranota* sp. (di), *Glossosoma* sp. (Gl), *Baetis* sp. (Bae), Acari (ac) and *Ephemerella ignita* (Eig) (Fig. 4:3).

Results from the summer survey at 50cm depth (Model 3) identified three significant variables: sulphate, geology and calcium (Table 4.2). The amount of variation explained by the significant variables is 5.45%. The first variable selected was sulphate (eigenvalue = 0.150), explaining 52.2% of the variation between the constrained variables, followed by geology (eigenvalue = 0.085, 30.3%) and calcium (eigenvalue = 0.039, 17.5%). The first three axes of Model 3 were highly significant ($p < 0.01$). The small percentage of variation explained by the three pCCA models is usual for species rich datasets where large numbers of zeros occur (Curtis et al. 2009).

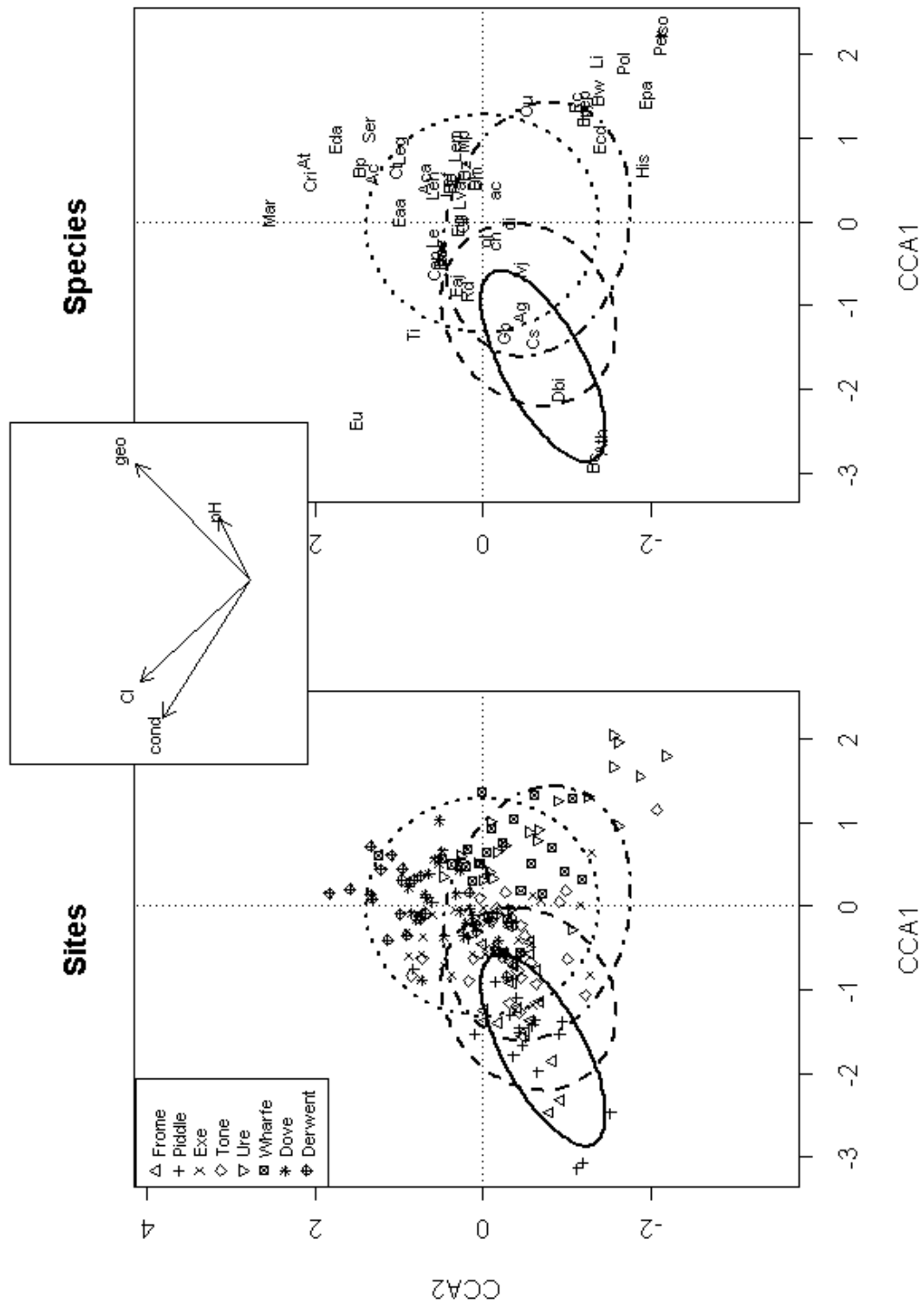


Figure 4:3. Partial constrained ordination (pCCA) of invertebrates collected from the summer sampling survey (2008) from 20cm depth. The significant environmental variables were chosen using forward selection and Monte Carlo permutation test ($P < 0.05$). For the identification of species codes see Appendix 2. Ecological variation between each geological area is depicted by confidence ellipses (95% confidence limit). Key: Chalk geology - ellipse with solid border, sandstone geology - ellipse with dashed border, limestone (Yorkshire Dales) - ellipse with dot-dashed border and limestone (Peak District) - dotted border.

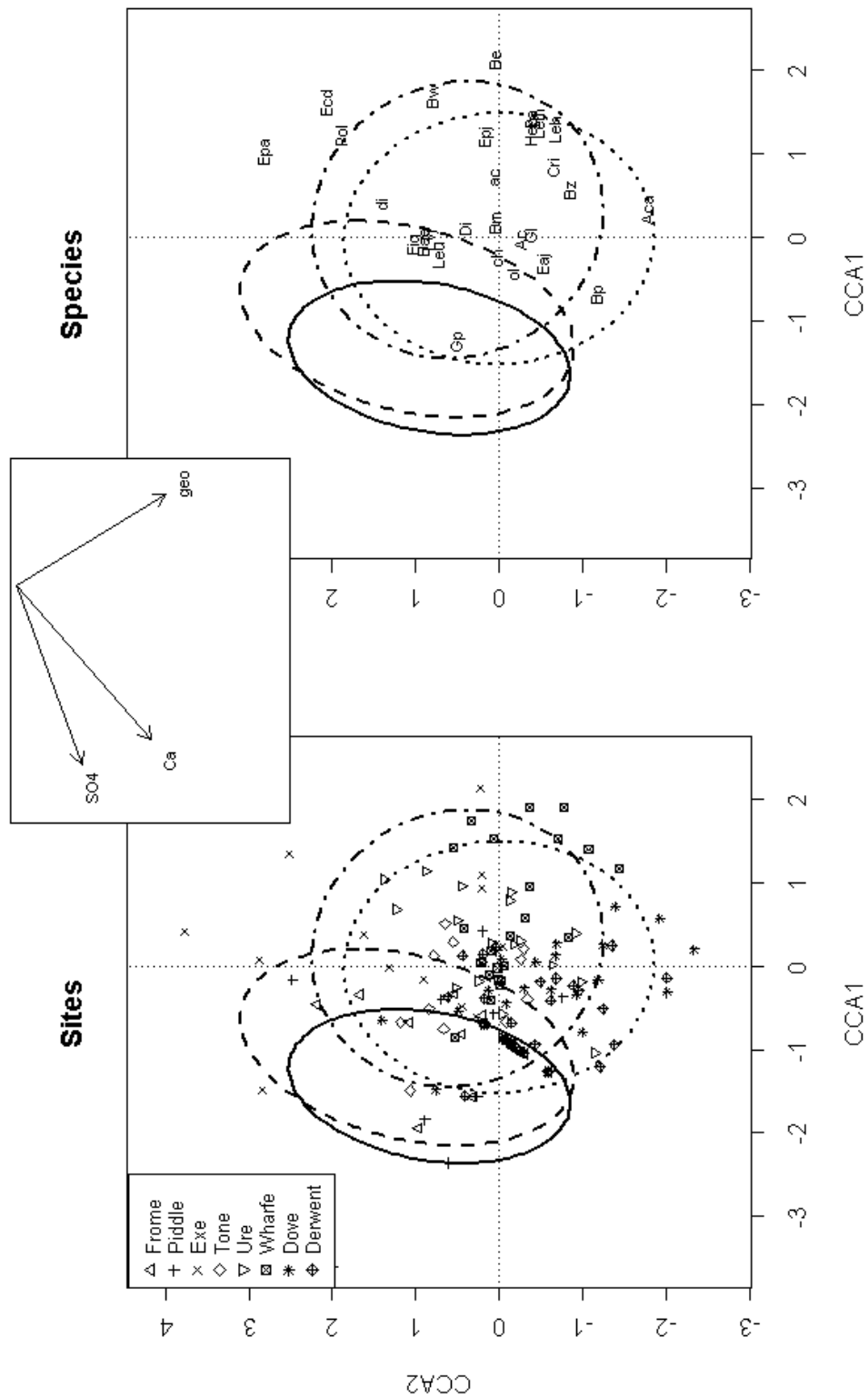


Figure 4:4. Partial constrained ordination (pCCA) of invertebrates collected from the summer sampling survey (2008) from 50cm depth. Species data is weighted and includes abundance values. The significant environmental variables were chosen using forward selection and Monte Carlo permutation test ($P < 0.05$). Ecological variation between each geological area is depicted by confidence ellipses (95% confidence limit). For identification of species codes see Appendix 2. Key: Chalk geology - ellipse with solid border, sandstone geology - ellipse with dashed border, limestone (Yorkshire Dales) - ellipse with dot-dashed border and limestone (Peak District) - dotted border.

Model 3 includes abundant species collected from 50cm depth from the summer sampling survey (2008) with outlying rarer species identified in Model 1 removed from the analysis. Sulphate (1st axis) and geology (2nd axis) explained the most variation within model 3 (Table 4.2, Fig. 4.4). Sulphate concentrations were high at both limestone river catchments in the Peak District (Dove and Derwent). Geology was again positively correlated with limestone catchments with the chalk and sandstone catchments negatively associated with the geology gradient. Samples collected from 50cm depth contained few characteristic species indicative of the chalk catchments with only *G. pulex* (Gp) falling within the confidence ellipse (Fig. 4:4). The sandstone sites contained more species within the confidence ellipse with *Leuctra* sp. (Leu), *Baetis* sp. (Bae) and *E. ignita* (Eig) common in the sandstone sites (Figure 4:4). Species ubiquitous to all sites occurring at the centre of the ordination plot include: Chironomidae, Oligochaeta, *Glossosoma* sp., *Dicranota* sp. and *Bryocamptus minutus* (Fig. 4:4). The limestone areas of the Peak District and Yorkshire Dales again have similar species compositions with both confidence ellipses large and containing many species.

Results from the winter survey at 50cm depth (Model 4) identified four significant variables: sulphate, pH, magnesium and geology (Table 4.2). The amount of variation explained by the significant variables is 8.65%. The first variable selected was sulphate (eigenvalue = 0.228), explaining 58.3% of the variation explained by the constrained variables, followed by pH (eigenvalue = 0.070, 18%) magnesium (eigenvalue = 0.065, 16.6%) and geology (eigenvalue = 0.028, 7.1%). The first three axes of Model V2 50cm were highly significant ($p < 0.01$). Model 4 includes abundant species collected from 50cm depth from the winter sampling survey (2008) with uncharacteristic outlying rare species identified in Model 1 removed from the analysis. Sulphate (1st axis) and pH (2nd axis) explained the most variation within model 4 (Table 4.2, Figure 4.5).

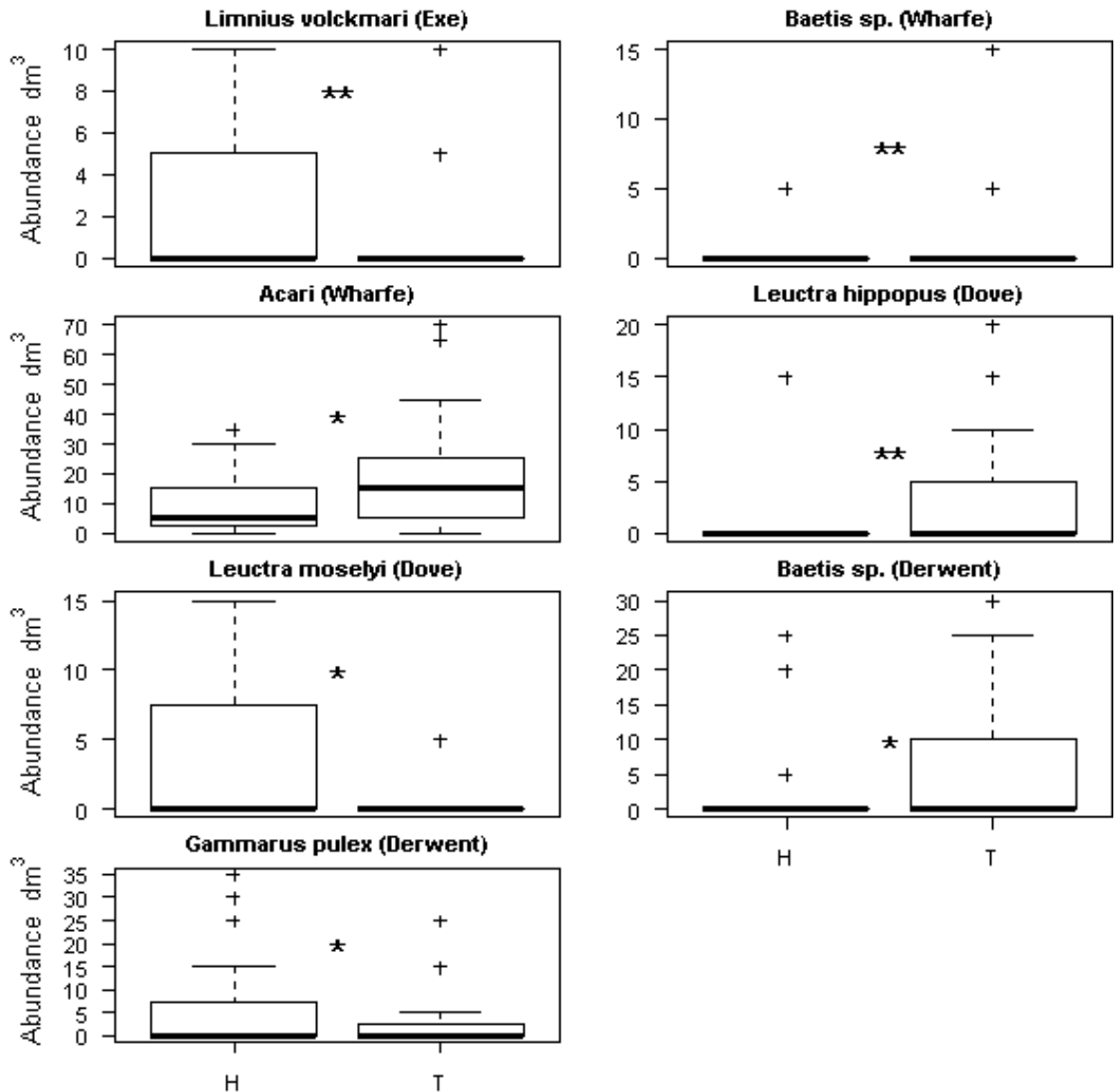


Figure 4.6. Abundance of dominant macroinvertebrate fauna collected from the head (H) and tail (T) of riffles during the summer sampling survey (July 2008). River catchments are given in brackets. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified Boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by error bars with distance calculated as 1.5 times the interquartile range. Significance values indicated by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

Similar to the summer survey at 50cm depth sulphate was a strong predictor of the variation in species data, in particular variation within the species data of the two limestone areas with sulphate concentration again high at the Peak District sites. pH was positively correlated with geology with both pH and geology positively correlated with the limestone areas and negatively correlated with the chalk and sandstone geologies. The two limestone areas share

similar species assemblages with both confidence ellipses large and occupying similar a space on the plot (Fig. 4:5). The greatest shift in species assemblages at the limestone sites from low to high groundwater levels is the increased abundance of *B. zschokkei*, (*Bz*) *B. minutus* (*Bm*) and *B. echinatus* (*Be*) in the Yorkshire dales catchments. Conversely the abundance of *B. zschokkei*, *B. minutus* and *B. echinatus* reduced from low to high groundwater levels in the Peak District sites (Fig. 4:5; Appendix 3). During the winter sampling survey chalk and sandstone catchments had similar species characteristics (Figure 4:5). Species such as *Attheyella wulmeri* (*Aw*), *Attheyella wierzejskii* (*Awi*) were only found in the chalk and sandstone sites, with two species particularly characteristic of the chalk and sandstone hyporheic were *Gammarus pulex* (*Gp*) and *Agapetus* sp. (*Ag*) (Fig. 4:5).

Cyclopoid species were represented by *Acanthocyclops* sp. (*Aca*) and *Diacyclops* sp. (*Di*) with *Diacyclops* sp. occurring across all geological areas, in particular the limestone catchments and the Exe catchment (Fig. 4:5). The Cyclopoida *Acanthocyclops* sp. was abundant in the Wharfe, Ure and Derwent limestone catchments (Fig. 4:5). Members of the Elmidae family differed in their distribution with *E. parallelepipedus* (juvenile and adults) particularly abundant in the Yorkshire dales sites. Whereas, the Elmidae species *Limnius volckmari* occurred consistently across all river catchments at 50cm depth, although highest abundances were also at the Yorkshire dales sites. (Fig. 4:5). Other macroinvertebrate species *Chloroperla trispinosa* and *Heptagenia* sp. are common and abundant across the limestone sites, particularly in the Yorkshire dales (Fig. 4:5). Species ubiquitous to all sites are again Oligochaeta, Chironomidae and Acari and collected at all catchments (Fig. 4:5).

Table 4.3. General linear model results of comparisons of abundance between riffles, head and tail of riffles (UD) and depths (20 and 50cm) during the summer survey (2008). Numbers given are t-values with associated statistical significant values (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Blank cells indicate no analysis undertaken due to insufficient species numbers. Key: Bz = *Bryocamptus zschokkei*, Bm = *B. minutus*, Be = *B. echinatus*, Nps = *Nitokra psammophila*, Di = *Diacyclops* sp., Aca = *Acanthocyclops* sp., Leh = *Leuctra hippopus*, Lem = *Leuctra moselyi*, Bae = *Baetis* sp., Gl = *Glossosomatidae*, Epj = *Esolus parallelepipedus* (larvae), Lvj = *Limnius volckmari* (larvae), Gp = *Gammarus pulex*, ch = Chironomidae, ol = Oligochaetae and Spr = species richness.

Comparison	Bz	Bm	Be	Aca	Di	Leh	Lem	Bae	Gl	Epj	Lvj	Gp	ch	ol	Acari	Spr
Frome																
Riffle _(3,47)														2.301*		-2.768**
HT _(1,47)														0.543		-1.845.
Depth _(1,47)														-3.003**		-3.152**
Piddle																
Riffle _(3,47)														-1.504		-2.085*
HT _(1,47)														0.981		0.573
Depth _(1,47)														-2.115*		-2.540*
Exe																
Riffle _(3,47)					2.005.			2.205*								1.072
HT _(1,47)					1.231			0.985								-0.413
Depth _(1,47)					-2.035*			-2.512*								-5.511***
Tone																
Riffle _(3,47)																
HT _(1,47)																
Depth _(1,47)																
Ure																
Riffle _(3,47)	0.601	1.919.	1.523		-0.313	0.003	-1.283		2.204*	-0.264	-0.62		3.742***	3.149**		1.244
HT _(1,47)	0.002	-2.116*	1.67		0.936	-0.78	0.733		0.133	1.287	1.473		-1.507	0.42	2.009.	-1.461
Depth _(1,47)	-1.853.	-2.279*	-2.147*		-1.054	-0.715	-1.58		0.752	-1.664	0.009		-1.432	-3.445**	-5.195***	-2.766**
Wharfe																
Riffle _(3,47)	2.750**	2.138*	0.007		0.015	1.486	0.734	0.947	-0.092	0.93	-2.289*		-1.325	-2.957**	1.591	2.724**
HT _(1,47)	1.825	0.629	2.202*		-0.031	1.239	0.481	3.143**	1.983	-0.079	0.695		0.525	-1.843.	2.31*	1.23
Depth _(1,47)	-0.498	0.472	-0.363		-2.231*	-1.613	0.54	-2.644*	-1.161.	-1.888.	-0.349		2.193*	0.851	1.229	-0.481
Dove																
Riffle _(3,47)	-1.915.	1.987.	0.003	0.006	0.979	3.000**	-1.374		0.728		-1.254	2.227*	7.350***	2.823**	2.220*	1.509
HT _(1,47)	-1.561	-1.014	-0.012	-1.396	1.495	3.169**	-2.289*		-1.055		-0.512	0.786	1.661	-1.637	-1.53	-0.838
Depth _(1,47)	-2.903**	-1.7	-0.009	0.938	-2.604*	-2.434*	-1.996.		-2.364*		-0.762	-2.194*	-3.389**	-3.221**	-2.757**	-5.867***
Derwent																
Riffle _(3,47)	1.487	0.005	-2.313*	1.15	-1.916.			1.395	0.008		0.006	2.921**	2.515*	-2.589*	1.412	1.293
HT _(1,47)	0.066	0.895	1.116	-1.757.	1.353			2.449*	0.491		-0.196	-2.379*	-0.598	-1.147	0.44	-0.838
Depth _(1,47)	-2.976**	-2.268*	-0.008	-0.167	-0.246			-3.267**	-1.447		-2.632*	-3.111**	-3.457**	-3.797***	-2.111*	-5.867***

Table 4:4. General linear model results of comparisons of abundance between riffles and the head and tail of riffles (UD) within each river catchment during the summer survey (2008). Numbers given are t-values with associated statistical significant value (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Blank cells indicate no analysis undertaken due to insufficient species numbers. Key: Bz = *Bryocamptus zschokkei*, Bm = *B. minutus*, be = *B. echinatus*, Nps = *Nitokra psammophila*, Di = *Diacyclops* sp., Aca = *Acanthocyclops* sp., Ct = *Chloroperla trispinosa*, ch = Chironomidae, ol = Oligochaetae, ac = Acari and Spr = species richness

Comparison	Bz	Bm	Be	Nps	Di	Aca	Ct	ch	ol	Ac	Spr
Frome											
Riffle _(3,23)								-3.247**	1.268		1.302
UD _(1,23)								0.071	1.729		1.183
Piddle											
Riffle _(3,23)								-1.152	-5.512***		-4.985
UD _(1,23)								0.033	0.844		0.742
Exe											
Riffle _(3,23)				0.005	-0.872			-1.506	0.005		2.773
UD _(1,23)				-0.001	-1.466			0.033	0.518		-0.012
Tone											
Riffle _(3,23)								-2.960**	3.109**	-0.004	2.773
UD _(1,23)								0.065	1.329	1.205	0.061
Ure											
Riffle _(3,23)	0.008		1.576					4.315***	-1.778.	-0.970	2.269
UD _(1,23)	-2.873**		-1.477					-0.517	-0.873	-0.854	-1.351
Wharfe											
Riffle _(3,23)	-1.720	0.654	2.655			0.004	1.854	-1.256	-1.459	1.726	2.490
UD _(1,23)	-1.773	-1.773	-1.443			-1.509	0.948	-0.308	-0.069	1.587	0.467
Dove											
Riffle _(3,23)			-0.828		0.005			2.897**	4.651***	-0.077	-1.826.
UD _(1,23)			0.500		-1.368			0.123	2.080.	-1.094	0.117
Derwent											
Riffle _(3,23)			0.005					1.524	1.394		2.928
UD _(1,23)			-1.663					0.193	0.759		-0.239

Reach scale distributions of the hyporheos: longitudinal and vertical patterns across hydrogeological areas

Longitudinal patterns

No significant difference in species richness was observed between the head and tail of riffles across all river catchments during both seasons (Table 4.3 & 4.4). Significant differences were observed at the species level although patterns were inconsistent. Abundance of *Limnius volckmari*, *Leuctra moselyi* and *Gammarus pulex* was significantly higher in the head of riffles at the Exe, Dove and Derwent catchments, respectively (Figure 4.6). Whereas, abundance of *Baetis* sp. (Wharfe catchment), Acari (Wharfe catchment),

Leuctra hippopus (Dove catchment) and *Baetis* sp. (Derwent catchment) was significantly higher in the tail of riffles (Figure 4.6). Where significant differences were observed this was predominately on the limestone (Yorkshire Dales and Peak District) and the Exe river catchments where strong up- and downwelling patterns were also observed with no significant differences observed in both chalk streams and the Tone river catchment (Table 4.3).

Vertical patterns

Across all river catchments (except the Wharfe) species richness was significantly higher at 20cm than 50cm depth, with no significant difference observed in the Wharfe catchment (Table 4.3, Appendix 2). The abundance of all dominant taxa collected from the chalk and sandstone river catchments was significantly lower at 50cm than 20cm depth, except the Exe catchment where abundance of *G. pulex* was lower at 50cm depth and close to significance ($P = 0.06$) (Table 4.3, Fig. 4.7). Across the limestone catchments the dominant pattern was lower abundance of species at 50cm than 20cm depth. The general pattern was not as evident as observed in the chalk and Tone (sandstone) catchments, for example abundance of *Leuctra* spp. and *E. parallelepipedus* was not significantly different between depths in both the Ure and Wharfe catchments in the Yorkshire Dales (Table 4.3, Fig. 4.8). Interestingly, in the Wharfe catchment many species were in high abundance at 50cm depth with no significant difference in abundance observed between 20 and 50cm depth for *Limnius volckmari*, *Bryocamptus zschokkei*, *B. minutus* and *B. echinatus* (Fig. 4.8 and Fig. 4.9).

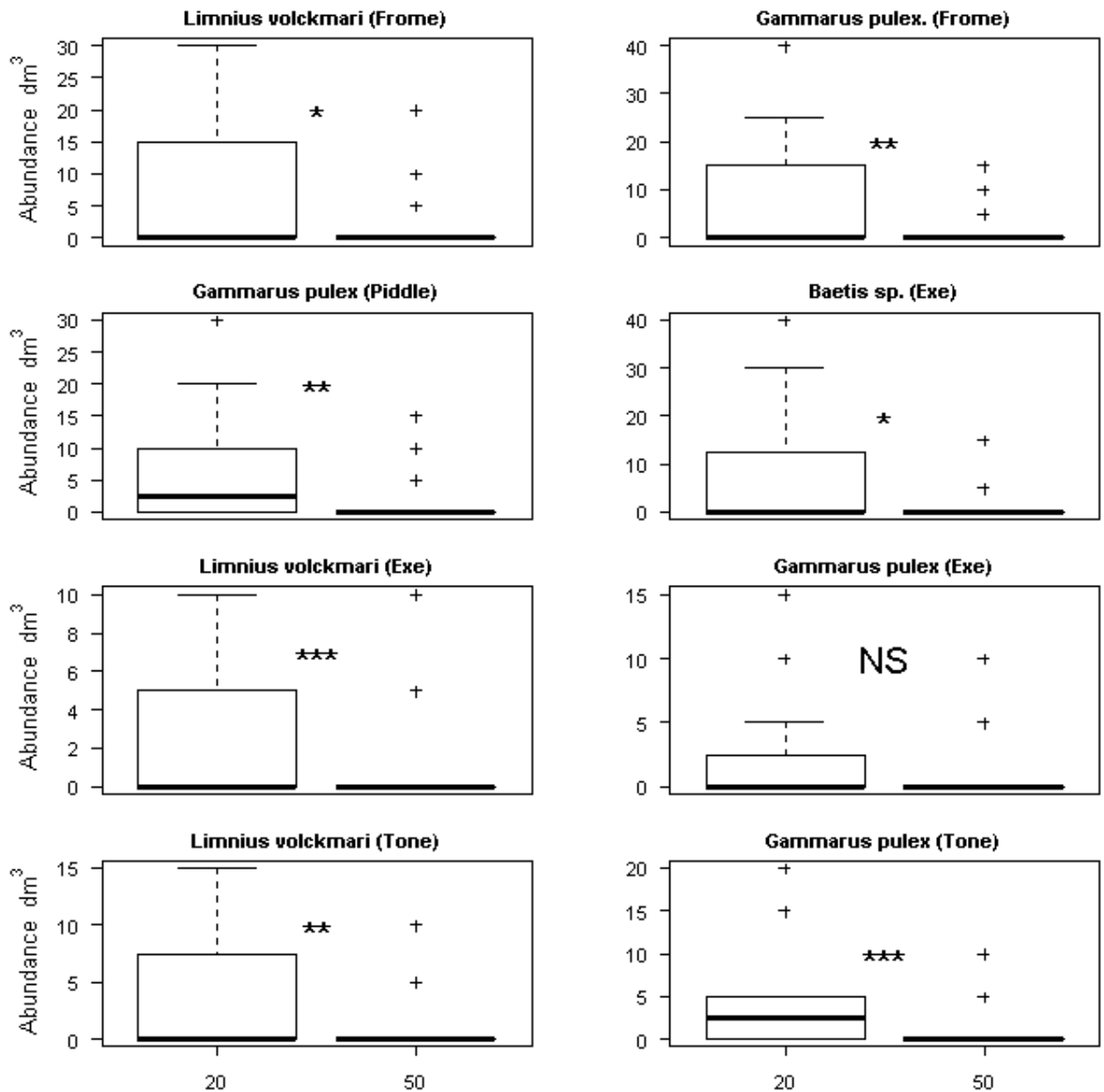


Figure 4.7. Abundance at two depths (20cm and 50cm) of the dominant macroinvertebrate taxa collected from the summer sampling survey (July 2008) from rivers with low hydraulic conductivity properties. River catchments are given in brackets. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Significance values are given by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

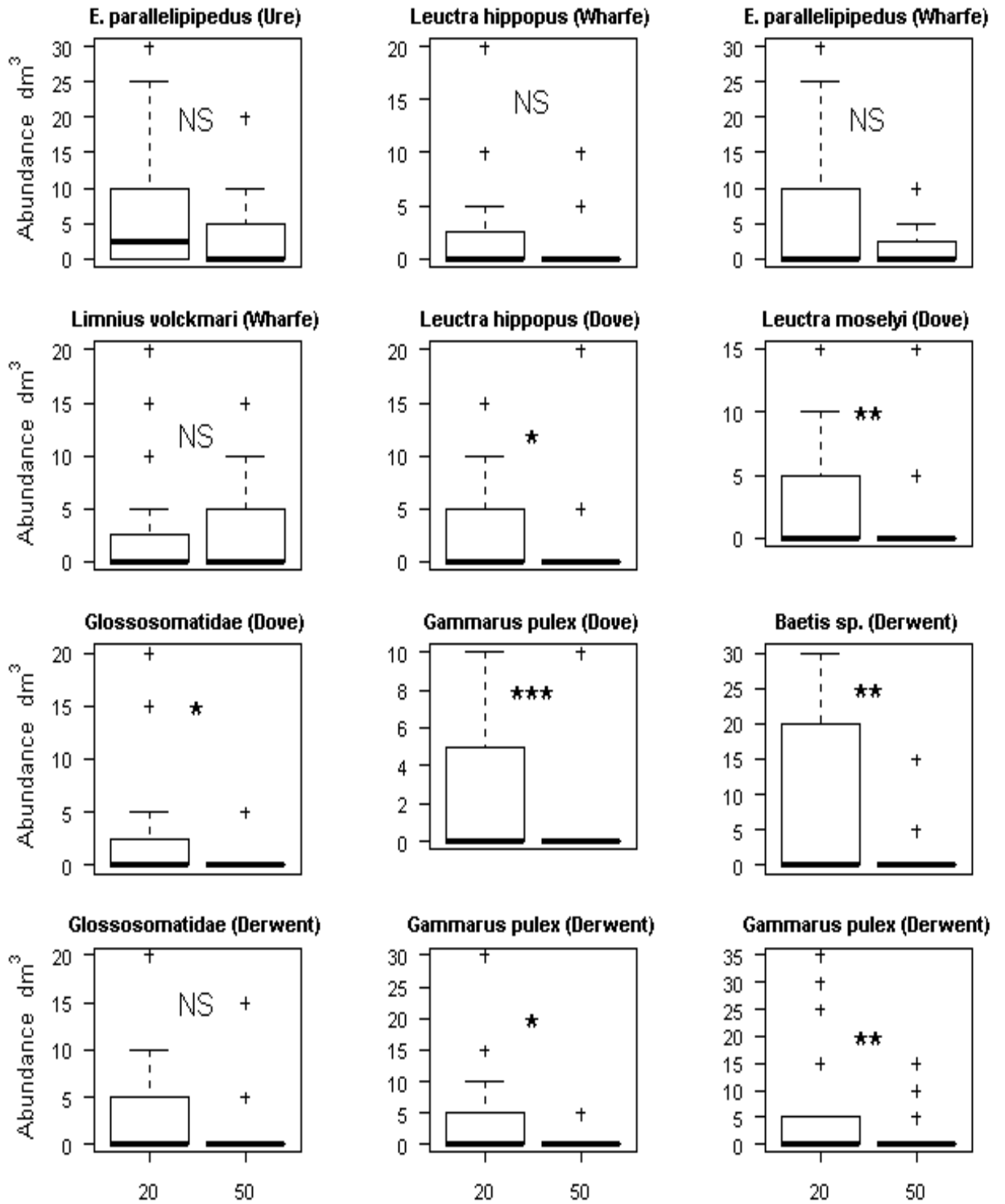


Figure 4.8. Abundance at two depths (20cm and 50cm) of the dominant macroinvertebrate fauna collected from the summer sampling survey (July 2009) from limestone river catchments. River catchment names are given in brackets. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Significance values are given by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

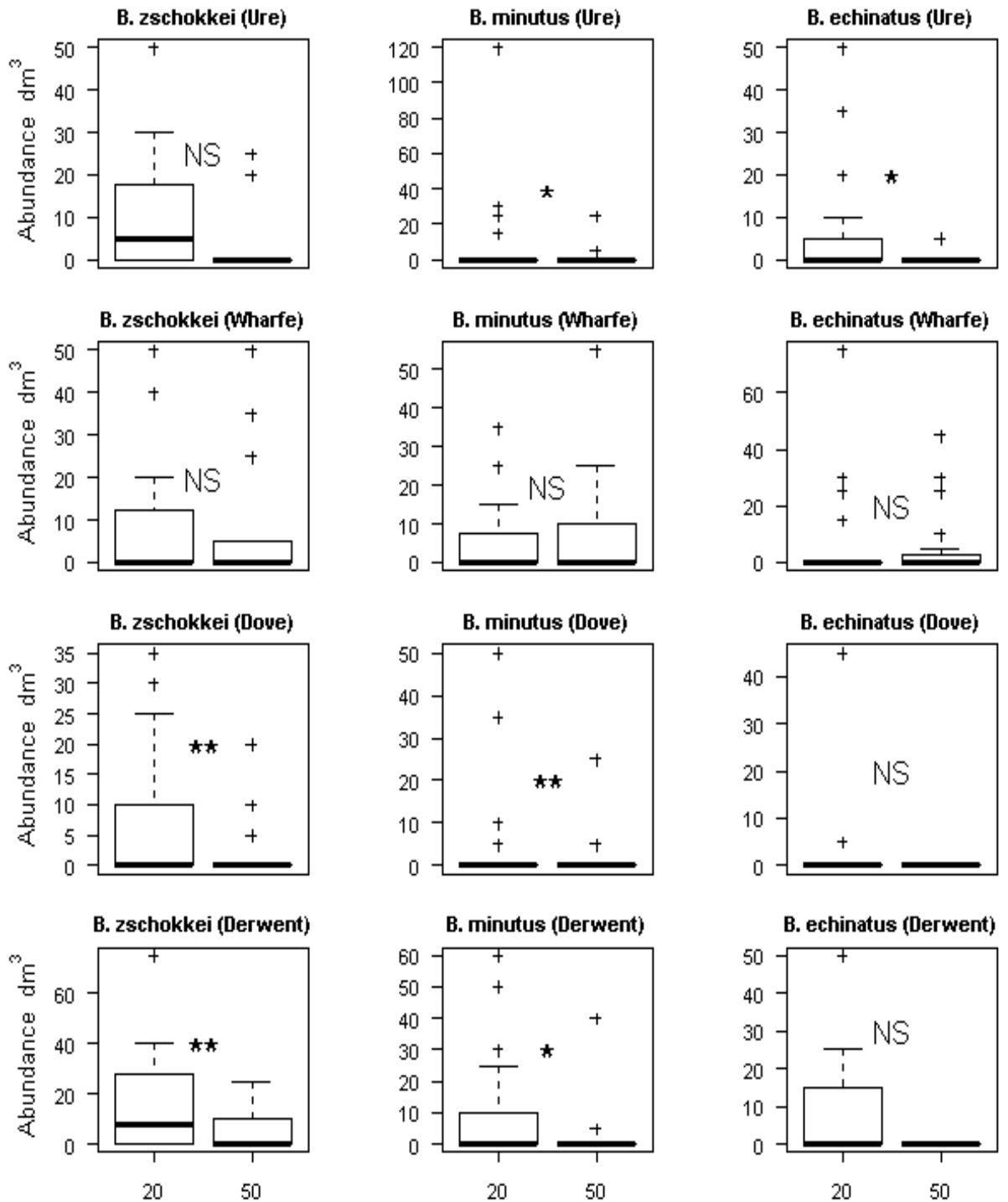


Figure 4.9. Abundance at two depths (20cm and 50cm) of dominant meiofaunal invertebrate species collected from the summer sampling survey (July 2009) from limestone river catchments. River catchment names are given in brackets. The central line in each box is the median residual (50th percentile) and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Significance values are given by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

Vertical distribution in body size of the hyporheos within river catchments: penetrability of riverbed sediments across hydrogeological regions

At both the Frome and Piddle chalk river catchments macroinvertebrate body size was significantly smaller at 50cm depth than at 20cm depth (Table 4.5, Fig. 4.10). Chironomidae body size was not significantly different between depths at both the Frome and Piddle (Table 4:5). In the Exe catchment Chironomidae body size was significantly smaller at 50cm depth than 20cm depth with significant difference in body size of macroinvertebrate and Harpacticoida observed between depths (Table 4:5). In the Tone catchment Chironomidae body size was significantly larger at 50cm than 20cm depth, with no significant difference in body size between depths observed for macroinvertebrates.

At the Ure limestone catchments in the Yorkshire Dales, Chironomidae and Harpacticoida body size was significantly smaller at 50cm depth than 20cm with no difference observed in the body size of macroinvertebrates between depths (Table 4:5). The Wharfe catchment macroinvertebrate body size was significantly smaller at 50cm than 20cm (Fig. 4.11), whereas difference was observed in body size between depths for both Chironomidae and Harpacticoida (Table 4:5). No differences in body size of macroinvertebrates, Chironomidae and Harpacticoida were observed at both Dove and Derwent Limestone River catchments in the Peak District (Table 4:5).

Table 4:5. ANCOVA analysis and regression parameters for relationships between body size (dependent) and abundance (predictor) between depths (co-variates). Numbers given are t-values with associated statistical significant value (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Blank cells indicate no analysis was undertaken due to insufficient species numbers. Depth (50cm) is compared to the baseline value - intercept (20cm) - positive and negative values of depth are relative to the baseline value (intercept) indicating if body size is higher or lower at 50cm depth than at 20cm depth.

Comparison		Macroinvertebrate		Chironomidae		Harpacticoida	
		intercept	t-value	intercept	t-value	intercept	t-value
Frome	Intercept (20cm)	4.026		0.825		NA	NA
	slope	-0.027	-1.022	-0.008	-1.998.	NA	NA
	Depth (50cm)	-0.864	-2.800**	-0.263	-0.634	NA	NA
	Degrees of freedom		1,97		1,57		
Piddle	Intercept (20cm)	4.334		1.183		NA	NA
	slope	-0.053	-0.994	-0.027	-0.582	NA	NA
	Depth (50cm)	-1.028	-2.288*	-0.494	-0.859	NA	NA
	Degrees of freedom		1,68		1,24		
Exe	Intercept (20cm)	3.836		1.020		-2.387	
	slope	-0.099	-1.623	-0.040	-2.386*	0.015	1.667
	Depth (50cm)	0.297	0.575	-2.176	-3.307**	0.230	0.761
	Degrees of freedom		1,77		1,43		1,29
Tone	Intercept (20cm)	2.947		-0.503		NA	NA
	slope	0.062	1.136	0.113	4.37***	NA	NA
	Depth (50cm)	-0.056	-0.103	3.201	2.667*	NA	NA
	Degrees of freedom		1,56		1,44		
Ure	Intercept (20cm)	3.160		3.378		-2.953	
	slope	-0.002	-0.127	-2.181	-9.486***	0.347	1.497
	Depth (50cm)	0.214	0.509	-1.125	-4.154***	-0.532	-2.719**
	Degrees of freedom		1,86		1,43		1,38
Wharfe	Intercept (20cm)	3.362		-0.204		0.021	
	slope	-0.054	-1.587	0.014	1.397	0.023	2.877**
	Depth (50cm)	-1.170	-2.515*	-0.681	-1.041	-0.002	-0.405
	Degrees of freedom		1,73		1,17		1,34
Dove	Intercept (20cm)	5.991		1.962		-2.579	
	slope	-2.123	-1.650	-0.954	-1.929	-0.009	-1.364
	Depth (50cm)	-0.223	-0.343	0.015	0.027	1.059	2.02.
	Degrees of freedom		1,120		1,62		1,32
Derwent	Intercept (20cm)	6.012		2.793		-3.196	
	slope	-3.268	-2.867**	-1.694	-6.057***	0.371	1.504
	Depth (50cm)	-0.641	-1.047	-0.168	-0.508	0.032	0.178
	Degrees of freedom		1,126		1,58		1,64

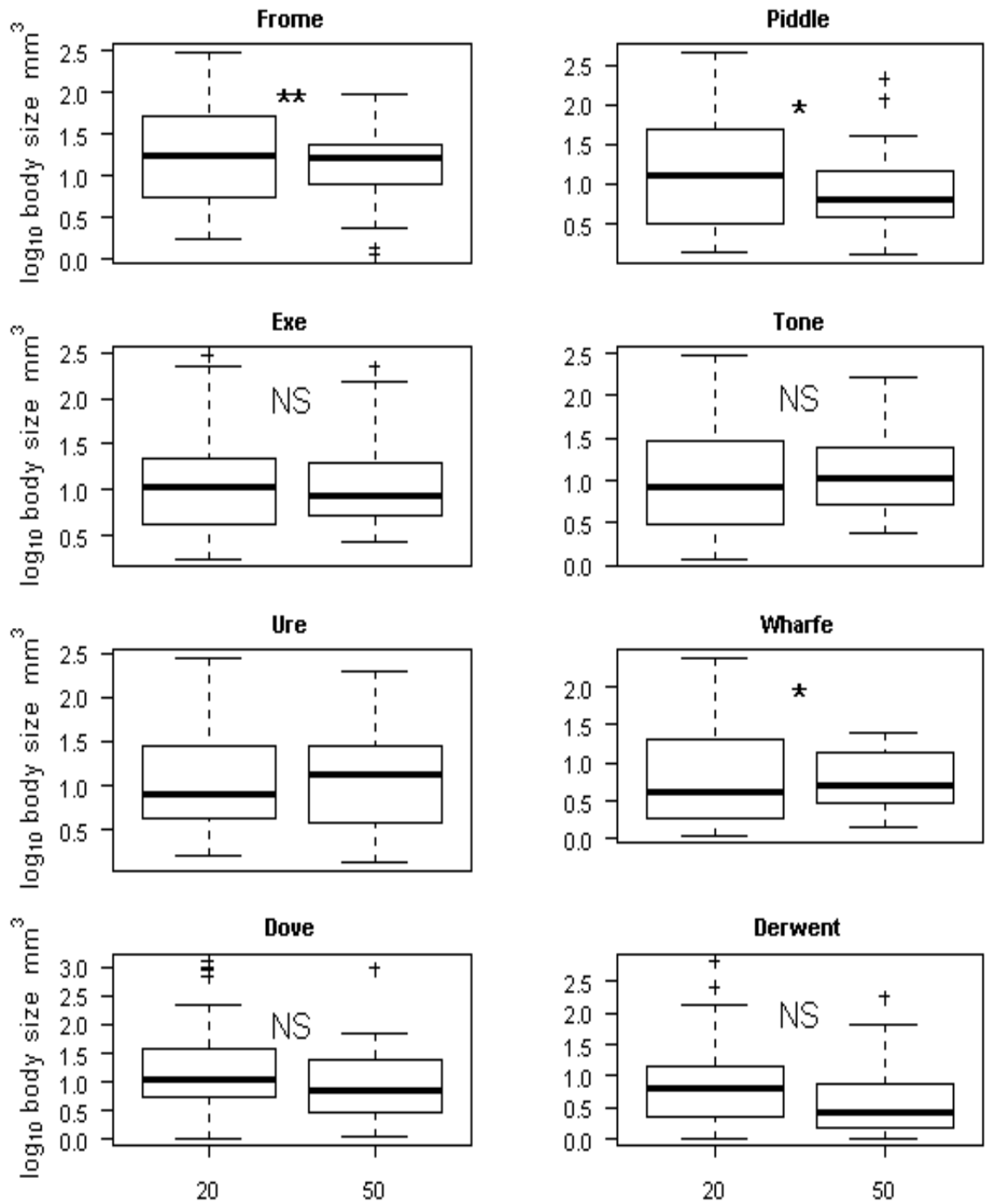


Figure 4.10 Body size (mm³) of macroinvertebrate sized fauna collected from 20cm and 50cm depths from the summer sampling survey. The central line in each box is the median residual (50th percentile) and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Data is presented from all river catchments. Significance values are given by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

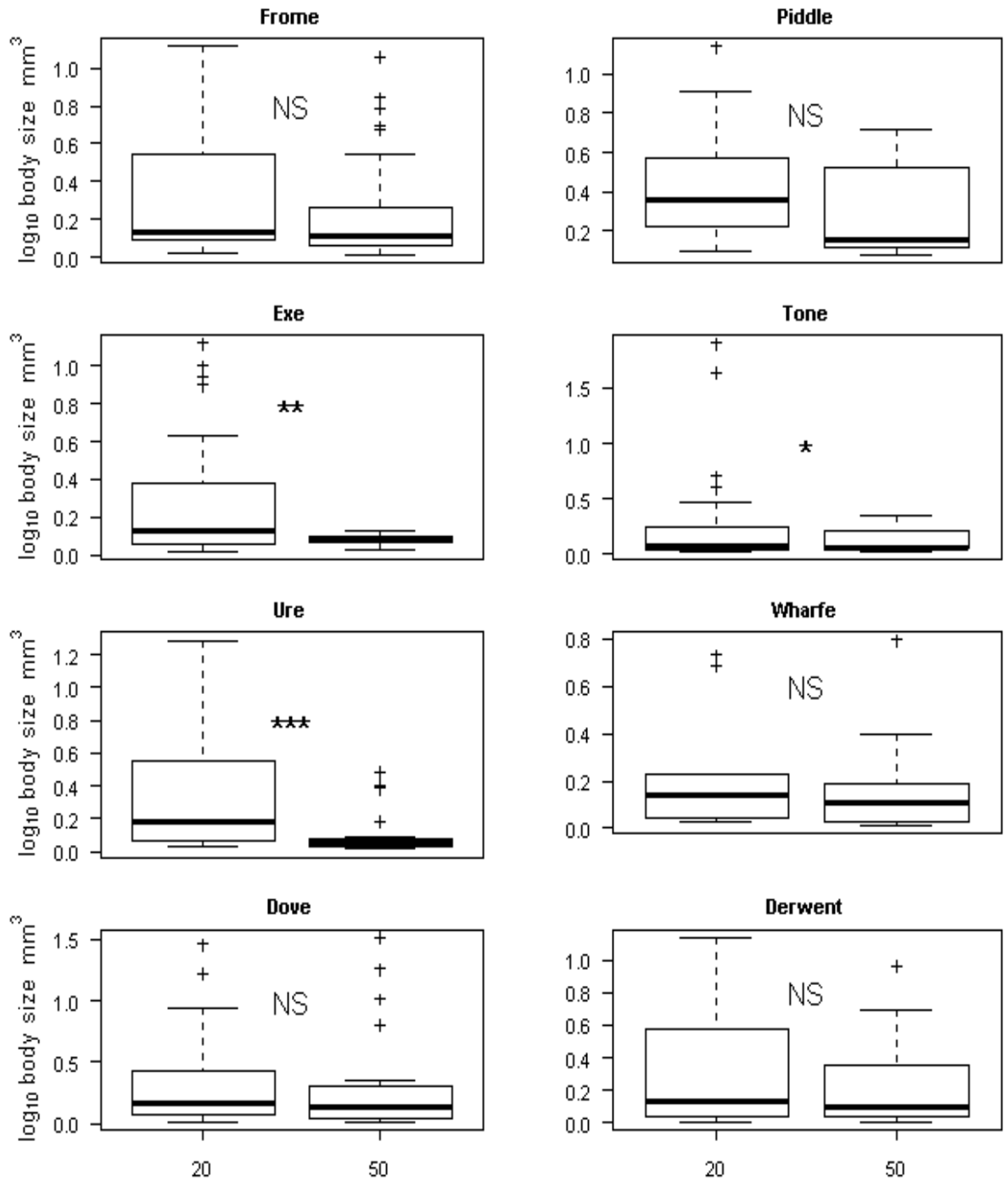


Figure 4.11. Body size (mm³) of Chironomidae larvae collected from 20cm and 50cm depths from the summer sampling survey. Data is presented from all river catchments. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Significance values are given by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant).

Size spectra of hyporheic communities across hydrogeological areas

There is no significant difference in the intercepts and slopes of meio- and macro invertebrate fauna between river catchments at both 20cm and 50cm depth from the summer sampling survey, and 50cm depth from the winter sampling survey (Table 4.6). At 20cm depth in the Frome catchment the slope was shallower than for all other catchments indicating a high abundance of large fauna and low abundance of small fauna relative to the other catchments (Table 4.7, Figure 4.12). Two limestone catchments also have shallow slopes (Wharfe and Derwent) again indicating a low abundance of small fauna and high abundance of large fauna relative to the other catchments (Table 4.7, Figure 4.12). At 50cm depth there was a shift in the size distribution with an increase in the abundance of small fauna at the negative end of the x-axis and a decrease in larger fauna at the positive end of the x-axis. The Wharfe catchment had the shallowest slope indicating the highest abundance of large fauna and lowest abundance of small fauna relative to the other catchments. The Frome catchment also had a shallow slope indicating large fauna are still relatively abundant at 50cm depth. The Piddle and Ure catchments had the steepest slopes with relatively high abundance of small fauna and low abundances of large fauna (Table 4.7, Figure 4.12).

Results from the winter sampling survey (Figure 4.13) show a shift towards the negative end of the x-axis with the majority of species of small body size, similarly the y-intercepts have all decreased except in the Wharfe catchment where the y-intercept has increased (Table 4.7). The Ure and Wharfe catchments had the shallowest slopes with relatively high abundances of large fauna and low abundance of small fauna (Table 4.7). The slopes for all other catchments were similar with similar proportions of large and small fauna.

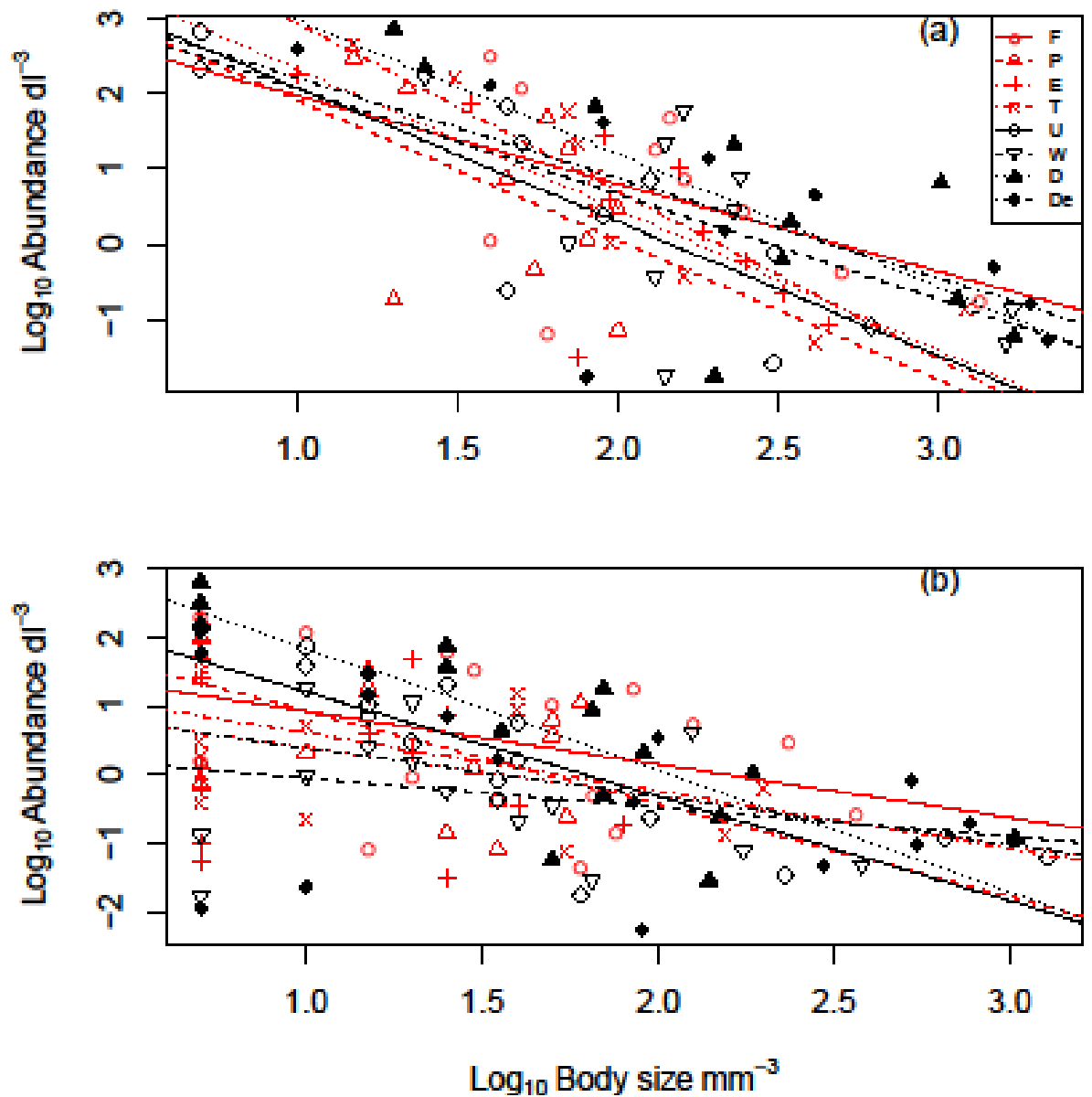


Figure 4.12. Plots of the hyporheic zone invertebrate size distribution for all river catchments. Data shown is for all meio- and macroinvertebrate fauna collected from the summer sampling survey (2008) from (a) 20cm depth and (b) 50cm depth. The steepness of the slope indicates the relative proportions of small and large invertebrates along the x-axis. Red slopes and symbols indicate chalk and sandstone geologies, black slopes and symbols indicate limestone geologies. Key: F = Frome, P = Piddle, E = Exe, T = Tone, U = Ure, W = Wharfe, D = Dove, De = Derwent.

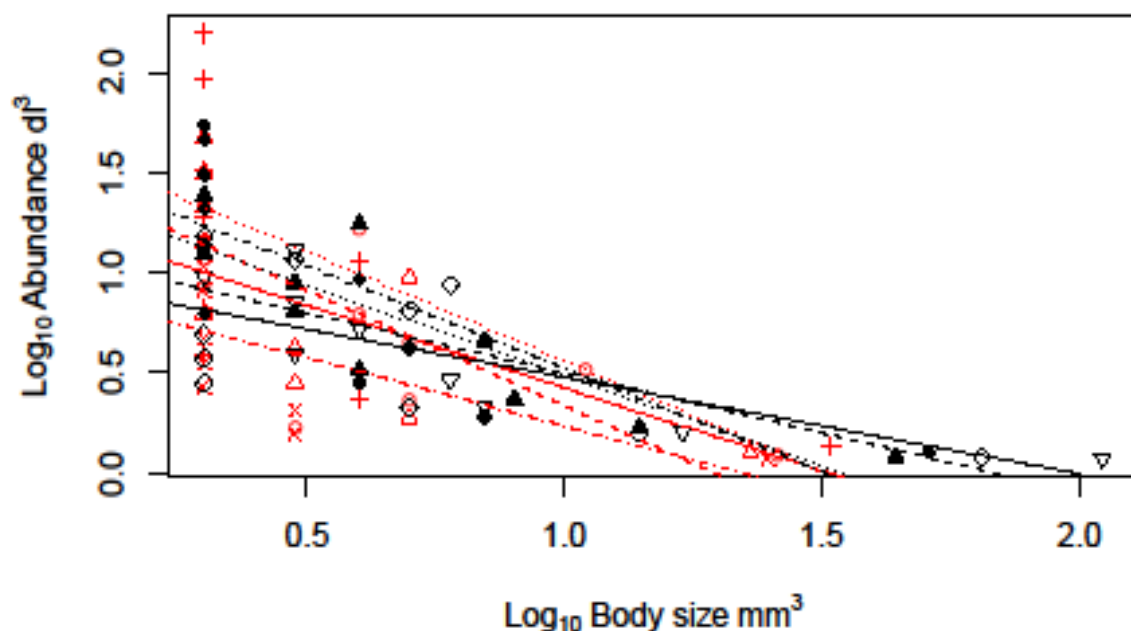


Figure 4.13. Plots of the hyporheic zone invertebrate size distribution for all river catchments from the winter sampling survey (2008). Data shown is for all meio- and macroinvertebrate fauna collected from 50cm depth. The steepness of the slope indicates the relative proportions of small and large invertebrates along the x-axis. Red slopes and symbols indicate chalk and sandstone geologies, black slopes and symbols indicate limestone geologies. For key to line types and symbols see Figure 4.12 plot (a).

Table 4.6. Analysis of covariance of the relationship between abundance and body size between river catchments.

	<i>df</i>	<i>SS</i>	<i>F- value</i>	<i>P-value</i>
Summer 20cm				
Body size	1, 64	59.79	58.27	<0.001
River catchment	7,64	1.036	1.009	0.432
Body size * river catchment	7,64	2.397	0.333	0.935
Summer 50cm				
Body size	1, 64	39.198	37.299	<0.001
River catchment	7,64	12.959	1.114	0.102
Body size * river catchment	7,64	8.197	1.114	0.359
Winter 50cm				
Body size	1, 64	8.444	68.279	<0.001
River catchment	7,64	1.774	2.049	0.062
Body size * river catchment	7,64	7.914	0.782	0.061

Table 4.7. Intercepts and slopes of body size distribution data for the summer (20cm and 50cm depth) and winter (50cm depth) sampling surveys.

River catchment	Summer 20cm		Summer 50cm		Winter 50cm	
	Intercept	Slope	Intercept	Slope	Intercept	Slope
Frome	3.1505	-1.1707	1.7605	-0.8038	1.2527	-0.8277
Piddle	3.8715	-1.9059	2.442	-1.4457	1.4853	-1.1487
Exe	4.2768	-1.9015	1.228	-0.7907	1.6507	-1.0904
Tone	5.2204	-2.2512	1.5461	-0.8914	0.9154	-0.6795
Ure	4.0241	-1.8532	2.804	-1.5534	0.9603	-0.482
Wharfe	3.4774	-1.4036	0.4528	-0.4709	1.0971	-0.5969
Dove	4.7853	-1.7866	3.7821	-1.8488	1.3901	-0.9015
Derwent	3.5688	-1.3401	1.1562	-0.7327	1.5444	-1.0228

Discussion

Influence of the Devensian glaciation on the regional distribution of the UK hyporheos

Evidence from Europe (Brancelj and Dumont 2007, Galassi et al. 2009b), North America (Strayer et al. 1995, Lewis and Reid 2007) and the UK (Robertson et al. 2009) supports the theory that recent glacial events affected the present day distribution of subterranean fauna. The results from this study support my hypothesis that stygobite species, in particular members of Niphargidae will be increasingly rare with increasing distance to the southern extent of the Devensian glaciation. The only true stygobite species collected from both limestone catchments was *Antrobathynella stammeri*. The high abundance of *Antrobathynella stammeri* collected in the Yorkshire Dales provides further evidence that this species is a glacial relict, with numerous records north of the Devensian glacial limit (Gledhill and Gledhill 1984, Stubbington et al. 2008). No specimens of *A. stammeri* were collected from the Peak District during this study, specimens were collected in a study running concurrently with this from the River Lathkill a tributary of the River Wye (Stubbington et al. 2008). Specimens of *A. stammeri* were also collected in this study from the Tone river catchment on the sandstone geology in Devon, and the River Lee a chalk stream in Hertfordshire (Octavian Pacioglu, *pers comm.*).

The distribution records of *A. stammeri* in the UK extend as far north as Stirlingshire with collected from the Altquhur Burn, a groundwater fed stream running off Old Red Sandstone (Maitland 1962). UK records of *A. stammeri* are commonly associated with areas associated with groundwater, although numerous specimens have been collected in the Lake District, where the geology is mainly volcanic rock, though interspersed with areas of calcareous sandstones (Millward et al. 2000). These sandstone areas occur along the west coastline of the Lake District, possibly providing a source population of *A. stammeri* and refugia from glacial effects on the surface. Migration upstream from these sandstone aquifers into the

Central Lake district could have occurred as sea levels rose with migration upstream into the central Lake District. All specimens of *A. stammeri* collected from the Lake District are from rivers running into the Irish Sea towards the sandstone aquifer running along the Lancashire coastline (i.e. St Bees head) (Gledhill and Gledhill 1984).

No evidence of *Niphargus* sp. was found in the two limestone catchments though there is evidence from the literature of *N. fontanus* in the carboniferous limestone areas of South Wales and the Mendips (Knight 2008). In this study *N. aquilex* had the broadest distribution with specimens collected across the Tone, Frome and Piddle catchments suggesting that the sample effort within each catchment was sufficient to detect all but the rarest species. The distribution of *N. aquilex* is well documented in the UK with numerous specimens occurring in routine Environment Agency sample collections (Knight 2008). The distribution of *Niphargus* sp. becomes notably patchier as you move north towards the Devensian glacial limit. There are a few records as far north as the Peak District, notably in Wales where specimens have been collected as far north as Anglesey (Knight 2008). Interestingly the current records north of the Devensian glacial limit are associated with rivers which run north to south (i.e. River Severn) whereas the two limestone areas sampled in this study feed rivers running in an easterly direction into the North Sea.

One particularly important record of *N. aquilex* is from the Afon Hirnant (Hynes 1961) located at the watershed of the Rivers Severn and Dee, with the watershed a possible migratory pathway between the Severn and the Dee and thus into North Wales. Records of Crangonyctidae (*Crangonyx subterraneus*) follow a similar distribution pattern to *N. aquilex* with distribution becoming patchier as you move towards the Devensian limit with many records located on tributaries of the River Severn (Knight 2008). The River Severn is the longest river in Great Britain providing a major migratory route for species capable of utilizing this migratory pathway. The close association of *N. aquilex* and *C. subterraneus* to

the River Severn's tributaries is strong evidence that the Severn is possibly the main west coast migratory pathway for these species following the last glacial extinction event.

The Harpacticoida had a broad spatial distribution with no species found exclusively north of the Devensian glacial limit. A few species were found only on the limestone catchments *Attheyella bidens*, *A. trispinosa* and *Moraria poppei*. The spatial distribution of *A. trispinosa* is widespread across Europe and the UK, with no European record of *A. bidens* found in the literature (de Jong 2010, Chad 2011). *Moraria poppei* has a Europe wide distribution with specimens collected in a few UK studies though the distribution is patchy, with a few specimens collected from mid Wales on the River Towy (Rundle and Ramsay 1997). One species in this study with a restricted distribution was *Nitokra psammophila* with specimens collected only from the Permo-Triassic sandstone sites in the Exe river catchment. The European distribution of *N. psammophila* is very small with records only for specimens in Germany (de Jong 2010). The distribution of *N. psammophila* is possibly wider in the UK and may have an affinity with sandstone geologies rather than a distribution restricted due to glacial affects.

Influence of hydrogeology on species-environment relationships in the hyporheic zone

The influence of fine sediment on the hyporheic invertebrate assemblage

The influence of granulometry is reported widely in the literature with a decrease in sediment size and interstitial space having a negative effect on abundance and species richness in the hyporheic zone (Strayer et al. 1997, Ward et al. 1998). A reduction in pore space due to clogging has also been shown to have a deleterious effect on abundance in the hyporheic zone (Bruno et al. 2009). Studies undertaken on chalk streams support this theory with reduced pore space resulting in low abundances of macrofauna (Davy-Bowker et al. 2006) and meiofauna (Tod and Schmid-Araya 2009) in alluvial sediments. Granulometry also influences the breakdown of organic matter with shredders often excluded when pore space

becomes too small (Navel et al. 2010b). The results from my study partly support my hypothesis that fine sediment will reduce species richness and abundance of invertebrate fauna in the hyporheic zone. At the species level the influence of fine sediments on invertebrate fauna was mixed with large macroinvertebrates (*G. pulex*, *L. volckmari*) and stygobite fauna (Niphargidae) abundant, whereas small meiofauna were low in abundance. The lowest hydraulic conductivity and highest percentage of fine sediments occurred in the Frome, Piddle and Tone river catchments. The Exe catchment did not fit the pattern of the three aforementioned catchments, having a low percentage of fine sediments. Alluvial sediments containing a high proportion of fine sediment and subsequently small interstitial spaces should restrict access into the hyporheic zone for larger macroinvertebrates.

The high abundance of *G. pulex* and *L. volckmari* in the hyporheic zone is unexpected, in particular *G. pulex* being the dominant fauna in the chalk catchments (apart from Chironomidae and Oligochaetae). Chalk and sandstone rivers are rich in macrophytes, therefore the high abundance of *G. pulex* in these rivers is unsurprising, with studies showing *Gammarus* sp. utilizing macrophytes for both habitat (Harrison et al. 2005) and feeding (Joyce and Wotton 2008). Also *L. volckmari* feeds largely on algae and detritus (Elliott 2008), and *Niphargus* sp. feed predominately on FPOM derived from the breakdown of CPOM (Navel et al. 2011), both species potentially benefitting the breakdown of CPOM by *G. pulex*. Studies have shown *N. rhenorhodanensis* feeding on FPOM produced by epigeal gammarid shredders, showing how two species occupying adjacent habitats can be symbiotic (Navel et al. 2011).

The abundance of *Niphargus* sp. in fine sediments has also been found in other studies with the ability to burrow into sediments observed in response to hydrological events (Dhomp-Avenas and Mathieu 1983, Dole-Olivier et al. 1997). Similarly stygobite *Crangonyx* sp. will also actively burrow through soft sediments when conditions allow (Holsinger and Dickson 1977). Vertical profiles have also been observed, with the abundance of the continental

amphipod *Niphargus rhenorhodanensis* greater at depth than the isopod *Proasellus valdensis* (Mathieu et al. 1992), similarly Marmonier et al. (2010) found hypogean organisms (*Niphargus* sp., and *Proasellus* sp.) more abundant at depth (50cm), whereas epigean fauna (*Gammarus* sp., Plecoptera and Ephemeroptera) were more abundant at the surface (15cm). These studies show separation between stygobite species and between stygobite and stygoxene species groups suggesting that *G. pulex* and *Niphargus* sp. may also be closely linked, although further investigation is required to ascertain the strength of the link.

The influence of coarse sediment on the hyporheos

The influence of sediment on hyporheic zone and surface water connectivity has long been accepted (Triska et al. 1989), with ecotones in the karst hyporheic highly dynamic and exhibiting high connectivity between groundwaters and surfacewater (Vervier and Gibert 1991, Plenet and Gibert 1995), with dissolved oxygen levels high (Dole-Olivier et al. 2009b). Species richness and abundance has been shown to be positively related to the porosity of the bed sediments (i.e. sediment size) (Gayraud and Philippe 2003). The results from this study support similar research in this area (Gayraud and Philippe 2001, Hunt and Stanley 2003, Dole-Olivier et al. 2009b) with meio- and macroinvertebrate fauna in the hyporheic zone at high abundance at 20cm and 50cm depth in the coarse substrates than the fine substrates broadly supporting the hypothesis that increased interstitial space will increase both species richness and abundance. In particular: *L. moselyi*, *L. hippopus*, *Glossosoma* sp. and members of the Elmidae family were relatively abundant at 50cm depth in the limestone hyporheic zone.

Members of both Leuctridae and Elmidae families are commonly found in the hyporheic zone (Plenet and Gibert 1995, Brunke and Gonser 1999, Malard et al. 2003a, Davy-Bowker et al. 2006), with early instars utilising the hyporheic zone as a nursery when pore space allows fauna to ingress (Bretschko 1992, Radwell and Brown 2008). In a recent study,

Franken et al. (2008) showed Plecoptera growth and development increased in coarse sediments where fauna could disperse to sheltered habitats, whereas fine sediments restricted ingress to sheltered habitats and growth and development was reduced. Plecoptera are known to frequent the hyporheic zone particularly in upland streams (Silveri et al. 2008) with *Leuctra* sp. in particular capable of utilizing the hyporheic with morphological characteristics enabling penetration of the sediment interstices (Cornut et al. 2010). The use of the hyporheic zone by early instar predators has also been shown in studies on hyporheic food webs. Schmid and Schmid-Araya (2002) found early and later instars of predatory macrofauna switching their diets as larval instar stage increased. Both early instar *Plectonemia conspersa* and *Sialis fuliginosa* diets consisted of 53% meiofauna and 23% macrofauna with the rest of the diet made up of algae and detritus, with later instar diets of both *P. conspersa* and *S. fuliginosa* consisting of equal proportions of meio and macrofauna.

The abundance of early instar Glossosomatidae in the hyporheic zone is not often mentioned in the literature although early instars are collected in the hyporheic zone (Marchant 1988, Dole-Olivier 1998). In New Zealand streams the cased caddisfly (*Olinga feredayi*: Conoesucidae) is often found in the hyporheic zone at depths of up to 35cm (Burrell and Ledger 2003) with 96% of annual secondary production of *O. feredayi* occurring in the hyporheic zone (Wright-Stow et al. 2006). Marchant (1988) found Trichoptera species in particular early instar *Tamasia* sp. (Calocidae) in high abundance in the hyporheic zone (10-30cm), with 20% of the *Agapetus* sp. (Glossosomatidae) population inhabiting the hyporheic zone (10-30cm). A recent study has shown different species of *Rhyacophila* larvae exploiting sediments of different porosity, *Rhyacophila* sp. with a slender body shape and vermicular/wormlike movement (similar to members of the Leuctridae and Elmidae families) can exploit hyporheic habitats, whereas *Rhyacophila* species without these adaptations were restricted to the upper benthic layers (Taira and Tanida 2011).

The influence of fine sediment on the hyporheos

Studies on the hyporheic zones of English chalk streams have shown a sparsely populated hyporheic zone (Davy-Bowker et al. 2006), with the shallow epigeic zone dominated by macrofaunal biomass (Tod and Schmid-Araya 2009) and a sharp decrease in meiofaunal abundance in the top 10cm of the benthic sediment (Tod and Schmid-Araya 2009). The large number of *G. pulex* and *L. volckmari* would support this result with both species dominating at 20cm depth. Surprisingly, *G. pulex* and *L. volckmari* also dominated at 50cm depth even though abundance decreased significantly. Conversely, the abundance of the smallest invertebrate fauna collected in this study (Harpacticoida) was low relative to other river catchments. In lake studies, Harpacticoida densities have been shown to be closely correlated with an increase in oxygen concentration, with high densities of Harpacticoida suggested as a possible indicator of oligotrophic waters (Sarkka 1992). Oxygen concentrations were reduced in the hyporheic zone of the fine sediments relative to coarse sediments, though concentrations were still relatively high, particularly in the chalk hyporheic sediments. The possibility of a shallow hyporheic zone occurring in the fine sediments is a possibility with Pretty et al. (2006) suggesting that a thin, biologically productive layer occurs in the chalk sediments of the River Lambourne. If this is also the case in the Frome and Piddle river catchments then the BOU-ROUCHE method would not detect these small scale chemical gradients.

A number of studies have found copepod abundance to be strongly affected by sediment size and permeability (Fiasca et al. 2005, Robertson and Milner 2006, Dole-Olivier et al. 2009b, Schmid and Schmid-Araya 2010). Chalk streams in the UK are vulnerable to streambed sediment clogging linked to local farming practices with many catchments located in areas with intense arable farming (Walling and Amos 1999, Warren et al. 2009). Chironomidae are predominately sedentary and have been shown to contribute little to the declogging of sediments with their burrows limited to the surface layers of fine sediments where they

construct tubes for feeding (Nogaro et al. 2006). The effect of inputs of fine sediments to riverbeds will vary dependent on sediment composition (i.e. coarse sediments or fine sediments); Nowinski et al. (2011) showed that permeability of coarse sediments increased after one year, whereas fine sediments decreased in permeability. This was due to fine sediments getting flushed from patches of coarse sediment and redeposited in the patches of fine sediments, providing a negative feedback with fine sediments unable to flush themselves clean (Nowinski et al. 2011). Studies in marine systems have shown fine sediments to impact harpacticoid copepods with fine sediment hindering mobility and also sticking to their feeding apparatus (De Troch et al. 2006). The low abundance of Harpacticoida and Cyclopoida crustaceans could be due to the input of fine sediments to the chalk streams with fine sediment having a deleterious effect on copepod numbers.

Hypogean fauna require specific behavioural and morphological adaptations to persist in the hyporheic zone, features such as an elongate bodyform, heightened sensory receptors (elongated antennae/legs, increased tactile senses) and importantly burrowing ability, to proliferate in subterranean habitats (Ward et al. 1998). When interstitial space becomes small these adaptations will be limiting, subsequently small taxa will proliferate at the expense of larger taxa, in particular protozoa and ciliates replacing copepods in fine sediments (Baldock et al. 1983, Sleight et al. 1992). Rotifers have also been found to dominate fine sediments in karst areas where relative porosity will be high (Beier and Traunspurger 2003). Sleight et al. (1992) found the contribution of the protozoan community to overall mean biomass and production in a chalk stream decreased in coarse sediments compared to fine sediments, with similar results found in studies on sandstone and chalk streams with a six fold increase in ciliate abundance in the chalk stream compared to the sandstone stream (Reiss and Schmid-Araya 2008).

The switch to coarser granulometry could also indicate a switch in contributions of taxa to overall biomass and production. The shallow hyporheic zone is supported by field chemistry

data from certain UK chalk streams, indicating a shallow area of surfacewater-groundwater mixing with groundwater predominately upwelling in sections of the River Lambourne (Pretty et al. 2006). In a study comparing differences in community assemblage between gravel-bottomed streams and sandy substrates, Hunt and Stanley (2003) found cyclopoid and harpacticoid copepods dominating gravel-bottomed streams, whereas the community in the sandy bottomed streams was dominated by Chironomidae and nematodes. In studies on recently formed glacial rivers similar patterns also occur with harpacticoid abundance increasing in well sorted sediments, whereas abundance decreased in poorly sorted sediments where porosity and interstitial space decreases (Robertson and Milner 2006). The dominance of different sized assemblage groups across a range of sediment sizes is not a new idea (Hakenkamp et al. 2002, Boulton 2007). The results from this study suggest that when the proportion of fine sediment increases then in concordance with the literature Harpacticoida will reduce in abundance, possibly benefitting the protozoan community. This decrease in assemblage body size with decreasing interstitial space would hold true apart from the increased dominance of macroinvertebrate species, in particular *G. pulex* and *Niphargus* sp. which suggests that other factors such as burrowing ability, tolerance of hypoxia are also important in fine sediments.

Hydrogeological influence on the longitudinal and vertical distribution of the hyporheos

A number of studies have found strong longitudinal patterns in faunal abundance and species richness between the head and tail of riffles associated with up- and downwelling zones (Fowler and Scarsbrook 2002, Marmonier et al. 2010). Conversely, other studies have found a strong depth effect but weak longitudinal effect for faunal abundance and species richness in the hyporheic zone (Bretschko 1981, Davy-Bowker et al. 2006, Franken et al. 2007). Hypogean organisms such as *Niphargus* sp. and *Proasellus* sp. are commonly associated with upwelling zones (Marmonier et al. 2010) whereas epigeal fauna (*Gammarus* sp., Plecoptera and Ephemeroptera) are associated with downwelling zones (Marmonier et al.

2010). The results from this study did not support my hypothesis: i.e. epigean fauna will be associated with the head of riffles (downwelling zones), hypogean fauna will be associated with the tail of riffles (upwelling zones) and species richness will be greater in the tail of riffles (upwelling zones).

Patterns of differences in the abundance of fauna between the head and tail of riffles were inconsistent, although where differences occurred this was at river catchments characterised by coarse alluvial sediments and also during the summer when groundwater input dominated streamflow. Patterns were also only observed for macroinvertebrate fauna, for example *L. volckmari*, *L. moselyi* and *G. pulex* were higher in the head of riffles and *L. hippopus* and *Baetis* sp. were higher in the tail of riffles. The coarse catchments showed much stronger effects of up and downwelling water and it follows that these sites will display a greater variation in faunal abundance. Similarly for physicochemistry no consistent pattern was observed between the head and tail of riffle apart from the Exe catchment which followed the textbook pattern of high DO and low ion concentration in the head of riffle and low DO and high ion concentration in the tail of riffles. The Exe was also associated with coarse alluvial sediments suggesting that where patterns between the head and tail of riffles follow textbook examples then certain hydrological conditions will be the driver for these differences.

I found no significant differences in physicochemistry between the head and tail of riffles in chalk catchments and this is consistent with other studies reported in the literature suggesting that chalk catchments are dominated by groundwater with penetration of surfacewater occurring at shallow depths. In a study on the River Frome, Davy-Bowker et al. (2006) found no significant differences in family richness and total number of invertebrates between the heads and tails of riffles in the hyporheic zone at both 0.25m and 0.5m depths. The results from this study support these results with the chalk sediments driven by groundwater inputs rather than surface-groundwater mixing processes. The mixed results from this broad

scale survey are not unusual with examples from the literature showing mixed patterns of abundance in up and downwelling areas. In a similar study, Olsen and Townsend (2003) found taxon richness not to differ significantly between up- and downwelling zones, whereas Malard et al. (2003a) found density and taxon richness greater in groundwater dominated upwelling zones. These results suggest that scale of up and downwelling is important (riffle scale, reach scale, catchment scale) in determining differences between up and downwelling. Also the sediment composition will greatly affect the amount of groundwater-surfacewater mixing in the hyporheic zone with up- and downwelling patterns stronger on porous substrates, then weakening as fine sediment composition becomes proportionally greater.

Penetrability of hyporheic sediments of riffle habitats: the influence of hydrogeology on the body size of fauna in the hyporheic zone

The influence of body size on the distribution of macrofaunal and meiofaunal sized taxa between depths varied across geologies. Benthic invertebrates of macrofaunal size are commonly found in the hyporheic zone (Bae and McCafferty 1994), particularly members of the Plecoptera group (McElravy and Resh 1991, Malard et al. 2003a) but also some Trichoptera (Marchant 1995, Taira and Tanida 2011) and Ephemeroptera species (Williams and Hynes 1974, Marchant 1988, Datry 2011). Studies have shown abundance and species richness of benthic macroinvertebrates decreases with depth (Angradi et al. 2001, Storey and Dudley-Williams 2004, Varricchione et al. 2005). Interstitial pore space and body size as limiting factors will become increasingly important as fauna move deeper into the hyporheic zone, although other factors are also important (i.e. reduced light, dissolved oxygen and particulate organic matter) (Brunke and Gonser 1997). The results from this study partly support my hypothesis: i.e. an increase in depth into the hyporheic zone will lead to a decrease in the body size of macroinvertebrate fauna, whereas body size of meiofauna will consistent throughout the hyporheic zone. Macrofauna showed a consistent pattern across just under half the river catchments with body size reduced between 20 and 50cm in the

Frome, Piddle and Wharfe river catchments. Importantly this decrease in body size was most apparent in the Frome and Piddle catchments which were associated with fine sediment deposits.

The use of the hyporheic zone by early instar larvae is common in many gravel bed streams, where pore space is sufficient to allow ingress (Bae and McCafferty 1994, Omesova et al. 2008). The significant decrease in body size at the two chalk catchments is strong evidence of the barrier the chalk sediments provide to ingress by taxa. The dominant macrofauna in both chalk catchments were *G. pulex* and *L. volckmari*. Studies have shown *Gammarus* sp. to penetrate into the shallow hyporheic zone to escape perturbations such as drought (Wood et al. 2010), and up to 2 metres deep to escape from spates (Dole-Olivier et al. 1997). In a study on the River Wye a groundwater fed stream in Derbyshire, Pringle (1982) found female *G. pulex* body size to be significantly related to sediment size with body size decreasing as sediment size decreased. *Gammarus* are known to burrow into sediments and can leave extensive networks of unlined tubular burrows (Duck 1986). This ability to burrow helps connectivity between the hyporheic zone and surface water, while facilitating energy supply into the deeper sediment layers. *Gammarus* are voracious eaters and consequently supply FPOM through faecal pellets into the sediments (Joyce and Wotton 2008). The faecal pellets become available to smaller meiofauna and in particular in the chalk sediments Chironomidae (Romito et al. 2011).

In this study there was no consistent pattern of differences in body size for meiofaunal size taxa, although it must be stressed that this study did not take into account fauna smaller than 63µm such as protozoans and small meiofauna such as some nematode and rotifer species. Chironomidae body size was greater at 50cm than 20cm depth at the Tone catchment and greater at 20cm than 50cm depth at both the Exe and Ure catchments. Similarly Harpacticoida body size was greater at 50cm than 20cm depth in the Piddle catchment with the opposite occurring at the Ure catchment. This inconsistent pattern of increases and

decreases in body size with depth across catchments of both high and low permeability, would imply the effect of morphology appears to be of small importance in explaining the distribution of meiofaunal sized taxa within riverbed sediments. Rather it would appear that an ecological rather than a physiological explanation of distribution would explain depth distribution more accurately. Harpacticoida, Chironomidae larvae and to a lesser extent Cyclopoida, are all abundant in the benthos of many streams and rivers (Dole-Olivier et al. 2000). The paucity of the more mobile meiofauna e.g. Harpacticoida and Cyclopoida in the chalk sediments is unusual. Meiofauna in the chalk sediments are dominated by early instar Chironomidae consistent with results from other studies on the chalk hyporheic (Davy-Bowker et al. 2006). These results suggest that body size of macroinvertebrate fauna in the hyporheic zone is strongly affected by the proportion of fine sediments, although early instar Gammaridae and Elmidae can still proliferate in fine sediments. The body size of meiofauna while seemingly affected by fine sediment composition the results were inconsistent suggesting other factors are also influencing the distribution of meiofauna in the hyporheic zone.

The influence of hydrogeology on the community size spectrum

Successful colonisation of the hyporheic zone by both epigean and hypogean fauna is dependent on the ability of invertebrates to either penetrate the sediment interstice (body size/shape) or to displace sediment through burrowing. Benthic invertebrates will show a decrease in abundance and species richness as depth increases (Gibert et al. 1990), with production in the hyporheic zone dominated by chironomids and early instar benthic invertebrates, both common in the deeper sediment layers (Smock et al. 1992). My results did not fully support my hypothesis: i.e. that as sediment size increases the proportion of large bodied fauna will also increase resulting in the size distribution slope becoming progressively shallower. The results from the summer survey at 20cm depth broadly supported the hypothesis with fine sediments depauperate in macroinvertebrate fauna. The

results from the Frome suggest that large fauna are relatively abundant in the fine sediments, with sediment size alone insufficient to describe the size of species inhabiting the hyporheic zone. At 50cm in both the summer and winter sampling surveys the increased abundance of meiofauna relative to macrofauna is clear across all catchments.

As previously mentioned *G. pulex*, *L. volckmari* and *Niphargus* sp. were abundant in the hyporheic zone of catchments with fine alluvial sediments. Where fine sediments occur it would appear that species capable of burrowing can proliferate whereas for small fauna, such as Harpacticoida, movement through the sediment interstices may be difficult. Numerous studies have observed *G. pulex* migrating vertically in chalk sediment deposits (Stubbington et al. 2009, Wood et al. 2010) and limestone deposits (Stubbington et al. 2010) to escape perturbations (floods, droughts). The use of the hyporheic as refugia by macroinvertebrates will vary as sediment size varies. Elongate or small species capable of moving in between sediment interstices may outcompete larger and stockier individuals where coarse grained sediments dominate, whereas alluvial deposits dominated by fine sediments burrowing ability rather than size may give species a competitive advantage to escape from perturbations (floods, droughts, predation).

Seasonality unsurprisingly has a large influence on the body size of fauna collected from the hyporheic zone. There was a shift to the negative end of the x-axis at 50 cm depth during the winter survey, with the use of the hyporheic zone by early instar macroinvertebrates well documented (McElravy and Resh 1991, Smock et al. 1992, Schmid and Schmid-Araya 1997). In temperate streams, timing is critical in order to utilise productivity, regulated by seasonal changes in temperature and light cycles. Insect emergence and breeding in temperate rivers often occurs between May-June with eggs deposited during this period. Hatching early instar larvae can colonise the hyporheic zone, growing through the autumn when leaf fall occurs utilising this important energy input (Gessner and Chauvet 2002). The leaf processing continuum (Petersen and Cummins 1974) shows variation in the nutritional

quality of leaf litter provides a continuous supply of nutrients to invertebrate communities and these are available throughout the year in both the benthic (Richardson 1992) and hyporheic zones (Cornut et al. 2010, Navel et al. 2010).

The paucity of Harpacticoida in the chalk streams has been discussed in respect of clogging of sediments, although fish predation could also be reducing their numbers. Harpacticoida can be preferentially selected by juvenile fish during feeding (Coull 1990). A recent study showed bottom feeding cyprinids (*Cyprinus carpio*) and gudgeon (*Gobio gobio*) can impact meiofaunal sized nematodes in the upper sediment layers (Spieth et al. 2011). Harpacticoida may be restricted from migrating into the hyporheic zone then are prone to predation in the benthic sediment layers. Subtle changes in morphology have been observed due to the effect fish predation, a significant reduction in body size of Copepoda occurred where fish were present in a controlled experiment (Dineen and Robertson 2010). A reduction in size can be seen as a reaction to visual predation with larger individuals consumed more readily.

Conclusion

At a regional scale, increasing sediment size and hydraulic conductivity properties resulted in an increase in species richness, abundance and importantly the size and type of species found in the hyporheic zone. Fine sediments had a deleterious effect on Copepoda abundance, whereas larger macroinvertebrate species, for example *G. pulex* and *L. volckmari* were relatively abundant in the fine sediments, whereas laboratory studies have shown *Gammarus* sp. to be excluded in fine sediments (Weigelhofer and Waringer 2003a). Regional scale studies have shown that Copepoda dominate hyporheic zones containing a high proportion of coarse sediments (Hunt and Stanley 2003) supporting the results from this study. Results from this study highlight the importance of using both meio- and macroinvertebrate fauna in hyporheic studies, with different size classes varying in their response to sediment composition. Coarse sediments displayed a highly connected hyporheic zone with large fauna abundant at depth. Conversely, fine sediments displayed a weakly connected

hyporheic zone with species richness, abundance and body size of fauna decreasing with depth. While sediment size was a good predictor of hyporheic community spatial patterns for depth and geology, reach scale patterns showed considerable variability, particularly at the head and tail of riffles. No consistent patterns were found between the head and tail of riffle in this study in contrast to other studies (Dole-Olivier et al. 1997, Franken et al. 2001, Marmonier et al. 2010). Results from this study support the weak longitudinal patterns observed in other studies (Davy-Bowker et al. 2006)

The lack of stygobite fauna north and south of the Devensian glacial limit at the two limestone sites suggests that Niphargidae and Crangonyctidae are absent or rare in the Limestone areas of the Peak District and The Yorkshire Dales. My results support findings on mainland Europe (Martin et al. 2009, Stoch and Galassi 2010) and North America (Strayer et al. 1995, Lewis and Reid 2007) where migration of stygobite species post glaciation is slow. Migration northwards in the UK is also possibly hindered by the lack of river systems running in a southerly direction (i.e. the River Severn). These results highlight the importance of the hyporheic zone to streams and rivers (refugia, habitat, nursery), while also highlighting that hyporheic zones associated with fine sediments are particularly vulnerable as species richness and abundance of many meio- and macroinvertebrate fauna is low.

Chapter V: Influence of granulometry on meiofaunal/macrofaunal colonisation in a

Karst stream hyporheic zone

Abstract

The influence of granulometry on hyporheic zone processes is profound; sediment size directly influences water flow and consequently the uptake and replenishment of key ecosystem properties (e.g. dissolved oxygen (DO), nutrients and minerals). It is important to understand how hyporheic fauna are influenced by sediment composition, particularly as sediment size is an important factor controlling hyporheic communities, with habitat homogenisation (i.e. dominance of fine sediments) reducing the diversity and abundance of the hyporheos. In this study I manipulated sediment size in the hyporheic zone (30cm depth) of a karst stream using colonisation chambers (n = 48) and ran two replicate trials in October and November 2009 (n = 96). The chambers were filled with fine sediment (sand), coarse sediment (fine gravel), mixture of fine and coarse (sand-50%, gravel-50%) and natural hyporheic sediment from the experimental site which had a high proportion of coarse sediment. Therefore I had four treatments that were different in terms of pore space, total surface area available for biofilm colonisation and water flow regime. The abundance and average body volume of each species colonising the chambers was determined. Further, I measured water chemistry and the amount of loosely associated organic matter (LOM) in each chamber. I hypothesised that granulometry would influence the colonisation of hyporheic meio- and macrofauna through available pore space, water chemistry, water flow regime and accumulation of organic matter. I expected that the different sediment types would “attract” assemblages that differ in terms of taxon identity, abundance and range of body sizes. Granulometry of the sediment had no effect on water chemistry but significantly higher amounts (LOM) were found in the natural and coarse sediment compared to the other two sediment treatments. There were significantly higher abundances of Chironomidae and macroinvertebrate species (*Chloroperla tripunctata*, *Elmis* sp., *Leuctra* sp.) in the natural and coarse treatments compared to the fine, but harpacticoid copepod species did not differ significantly in abundance between treatments. I also found an effect of granulometry on faunal body size individuals within the Chironomidae and the plecopteran species *Chloroperla tripunctata* were on average larger in the coarse sediment compared to the other sediment types. These results suggest that an increased proportion of coarse sediments at the patch scale support a diverse and abundant hyporheic fauna. The relative proportion of meiofauna compared to macrofauna within the hyporheic community also increases in fine sediments with larger bodied taxa excluded; suggesting meiofauna may assume a greater role in ecosystem functioning in fine sediment.

Introduction

Sediment grain size is intimately related to the hydraulic conductivity of the substrate, as grain size (and pore space) increases so does hydraulic conductivity (water flow) (Sharp 1988, Hiscock 2007). Water flow is important in surface sediments and in the interface between the surface sediments and the ground water (the hyporheic zone, HZ) as the rate of flow governs the replenishment and uptake of minerals, nutrients and dissolved oxygen. In the HZ a decrease in sediment size results in a greater sediment surface area for colonisation by biofilms of heterotrophic bacteria. Therefore, decreased water flow and increase in biofilms will increase biochemical oxygen demand (Ferreira et al. 2009). The switch from oxic to anoxic conditions requires alternative terminal electron acceptors such as nitrate, influencing denitrification processes (Rivett et al. 2007, Navel et al. 2011a) and increasing biogeochemical processing rates (Wotton 2007, Datry et al. 2008, Schmid and Schmid-Araya 2010). Alternatively, in sediments with a high proportion of coarse material water flow will be greater, with inputs of oxygen from the surface supporting stygoxene taxa (Malard and Hervant 1999, Marmonier et al. 2010), salmonid larvae (Finn 2007, Ferreira et al. 2009) and diverse and abundant meiofaunal (Ward and Voelz 1990) and macrofaunal communities.

Organic matter in the hyporheic zone is derived from numerous sources, such as inputs from terrestrial and aquatic plants in the form of coarse particulate organic matter (CPOM), from biofilm development on sediment surfaces and the breakdown of CPOM to fine particulate organic matter (FPOM) through mechanical and biological processes (Wong and Williams 2010). The proportion of FPOM has been shown to increase with depth, as attenuation (due to filtration) of CPOM occurs within the sediment layers (Vervier et al. 1992, Brunke 1999). Surface shredders (Gammaridae) feeding on CPOM produce large amounts of FPOM that penetrates into the hyporheic zone (Joyce and Wotton 2008), providing a food source for hyporheic invertebrates. Due to the attenuation properties of fine sediments in the hyporheic

zone, FPOM and biofilm constitute a greater proportion of total organic matter content, whereas in coarse sediments CPOM will make up a relatively greater proportion of the total organic matter content.

Fauna which inhabit the HZ (hyporheos) are small-sized and separated into two categories: the meiofauna (pass a 500 μm sieve and are retained on a 67 μm sieve) and the macrofauna (that are retained on a 500 μm sieve). These organisms play an important role in the HZ sediments because they feed on organic matter and the microbial food web. The ecology of the hyporheos is generally not well understood (Robertson and Wood 2010), however a few studies have shown some general colonization patterns of hyporheic meio- and macrofauna. Meiofauna can penetrate through small sediment interstices and are often in higher abundance than macrofauna in the hyporheic zone, where interstitial space is reduced (Swan and Palmer 2000, Stead et al. 2004). In agreement with this study, Weigelhofer and Waringer (2003b) found that an increase in the percentage of fine sediments negatively influenced macroinvertebrate densities in the HZ. As interstitial space in the HZ becomes limiting to macroinvertebrates, access requires adaptations such as slender body shape and vermicular movement. Therefore the hyporheos often contains high numbers of macroinvertebrates such as stoneflies (Stanford and Gaufin 1974, Silveri et al. 2008), mayflies (Olsen and Townsend 2003) and caddisflies (Pepin and Hauer 2002, Burrell and Ledger 2003, Wright-Stow et al. 2006) which are often small or have elongate body forms.

These findings are not surprising because studies on surface sediment have also shown that the ability of fauna to inhabit the sediment is strongly influenced by granulometry. Within meiofaunal crustaceans, Cyclopoida are most abundant at medium- to coarse grain sizes in slow flowing subterranean streams, whereas Harpacticoida abundance is high in gravelly, sandy substrates (Galassi et al. 2009b). In coarse, gravelly substrates meiofaunal abundance and species richness can be high with over 300 species collected from the Oberer Seebach, Austria (Schmid and SchmidAraya 1997), but also in fine, sandy sediments where interstitial

space is reduced meiofaunal species richness can exceed 145 species (Hakenkamp and Palmer 2000). Benthic macroinvertebrate abundance can also be high in coarse, permeable benthic sediments, whereas fine sediments reduce macroinvertebrate diversity (Quinn and Hickey 1990, Lake 2000).

I chose to address colonisation of different sediment types in the hyporheic zone of a karst river to test whether meiofaunal colonization differs from that of macrofauna, whether body size was an important factor for colonization and which factors controlled colonization. I conducted an experiment using colonization chambers that were filled with four different sediment types and that were buried in the karst HZ. Karst environments and their subterranean habitats (caves) (Wood et al. 2008, Dole-Olivier et al. 2009a) and surface habitats (benthic) (Beier and Traunspurger 2003) are well studied, with hyporheic experimental research on karst often focused on macrofauna (Stubbington et al. 2010) with meiofaunal studies rare. Karst hyporheic zones are dynamic ecotones exhibiting high connectivity between surface waters and groundwaters (Dole-Olivier and Marmonier 1992), recently Culver and Pipan (2011) suggested the hyporheic zone of karst systems be classed as a shallow subterranean habitat as groundwater and surfacewater is so intimately connected. This high connectivity is intrinsically linked to water flow and responsible for the dissolution of fissures (karstification) within the epikarst and aquifer (Gibert et al. 1990). Subsequently, species richness and abundance in the karst hyporheic can be high with both epigeal and hypogean fauna abundant, as found for the karst hyporheic zones of two streams in the Peak District and Yorkshire Dales. The karst hyporheic therefore provides a unique opportunity to study faunal colonization patterns more rigorously than would be possible in other hyporheic environments where abundances can be too low to detect any general patterns. In detail, I tested the following hypotheses that were based on descriptions in the literature:

- (1) Concentrations of dissolved minerals will increase and dissolved oxygen decrease as the proportion of coarse sediments decreases.
- (2) Organic matter (LOM) input from the surrounding stream will be greater in sediments containing the greatest proportion of coarse sediments. Conversely, in fine sediments (i.e. sand) LOM will be low as attenuation of CPOM occurs.
- (3) Meiofauna will be more abundant than macrofauna in all sediment types, but where interstitial space is greatest (i.e. in coarse sediments) the proportion of macrofauna will be higher.
- (4) Body size of meiofauna will be similar across treatments, but body size of macroinvertebrate fauna will increase as the proportion of coarse sediments increases (because of interstitial spaces). Body size of meiofauna will be similar across treatments.

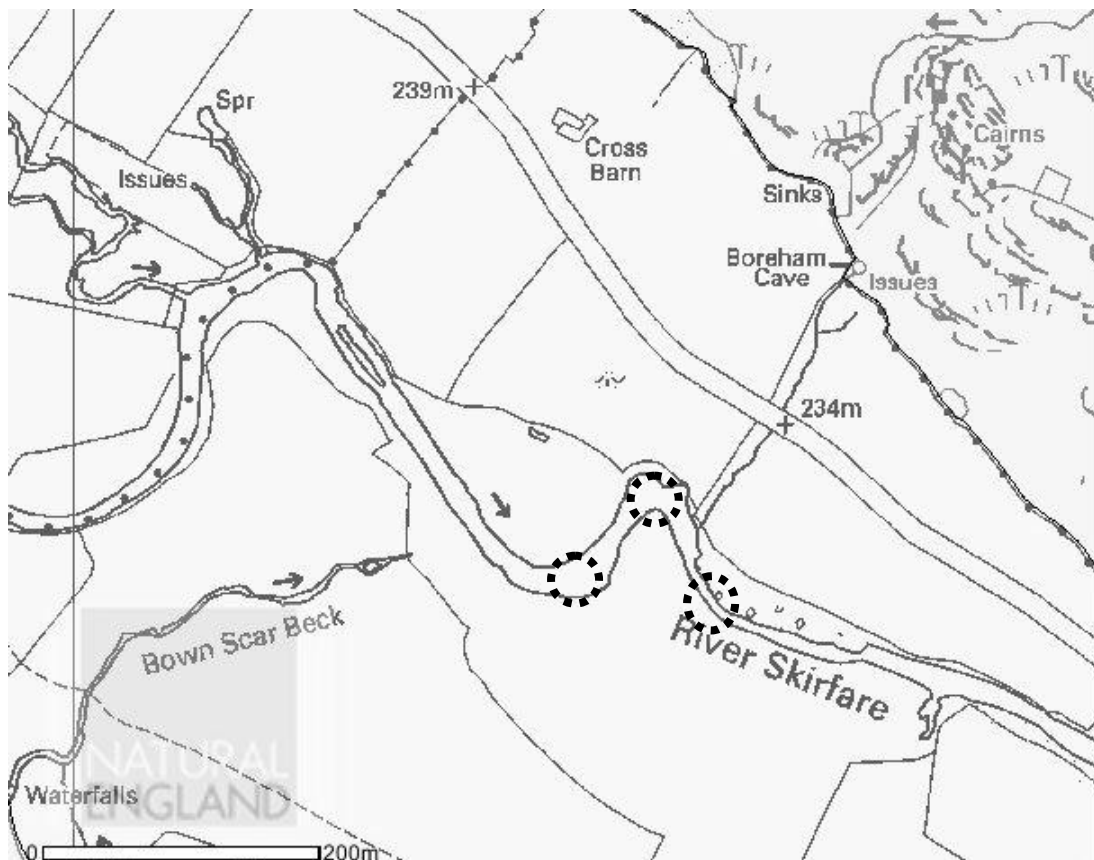


Figure 5.1. Map of the study area located on the River Skirfare, Yorkshire Dales National Park, UK. Colonisation chambers were buried in three riffles which are marked with dotted circles.

Method

Site description

The River Skirfare (Fig. 5:1), is located within the Yorkshire Dales National Park, North Yorkshire, UK (54:08:56 N, 2:07:12 W), an area underlain by carboniferous limestone manifested as a karst landscape. A detailed description of the study site is given in Chapter 2. The River Skirfare is a pristine UK river, surface water quality very good (Environment Agency, General Quality Assessment, chemical grade A, biological grade A). Anthropogenic nutrient enrichment is very low compared with national levels, primarily due to the low impact nature of hill farming in the Yorkshire Dales. The long term monthly average rainfall for October and November in the study area is 82mm per calendar month (Marsh and Sanderson 2009). During the second trial of this experiment an exceptional rainfall event occurred, in Northern England new UK rainfall records were set with 316.4mm of rain falling at Seathwaite, Cumbria on the 20th November 2009 (Sibley 2010). The study area was located 50 miles from Seathwaite and was similarly affected by the weather system with rainfall five times the monthly long term November average (Fig. 5.2) and riverflow on the River Wharfe was three times the November long term monthly average (Marsh and Sanderson 2009).

General experimental set-up

This experimental study incorporated two trials, one in October and one in November of 2009. Three riffles were selected for the study with similar bank width and depth located along a 300m section of the River Skirfare (Fig. 5:1). At the head of each riffle sixteen colonisation chambers were buried which represented four replicates of four treatments. The four treatments were: fine sediment (sand, f), coarse sediment (fine gravel, c), a mixture of fine and coarse (sand-50%, fine gravel-50%, m) and natural hyporheic sediment (n) which had a high proportion of coarse sediment. The chambers were inserted adjacent to each other

at a depth of 30cm, and left in situ for four weeks. Previous studies have shown this time is sufficient for faunal abundance in the chambers to be similar to that in the surrounding sediment (Boulton et al. 1991, Bo et al. 2006).

The experimental design gave 96 colonising chambers in total: 2 trials x 4 sediment treatments x 12 replicates (4 replicates within each of 3 riffles).

The colonisation chambers were approximately 1L in volume, with access to the internal sediment possible only from the sides (Fig. 5:4; Fig. 5.5). Each chamber had a tube inserted into the top which penetrated 4cm into the internal chamber. The tube end was covered with 63µm boulding silk to allow the withdrawal of water without removing fauna from the chamber. Water samples were taken from the chambers one day prior to removal of the pots to minimise disturbance of the fauna. Water samples were extracted using a syringe attached to the plastic tube connected to the inside of each pot (Fig. 5.4).

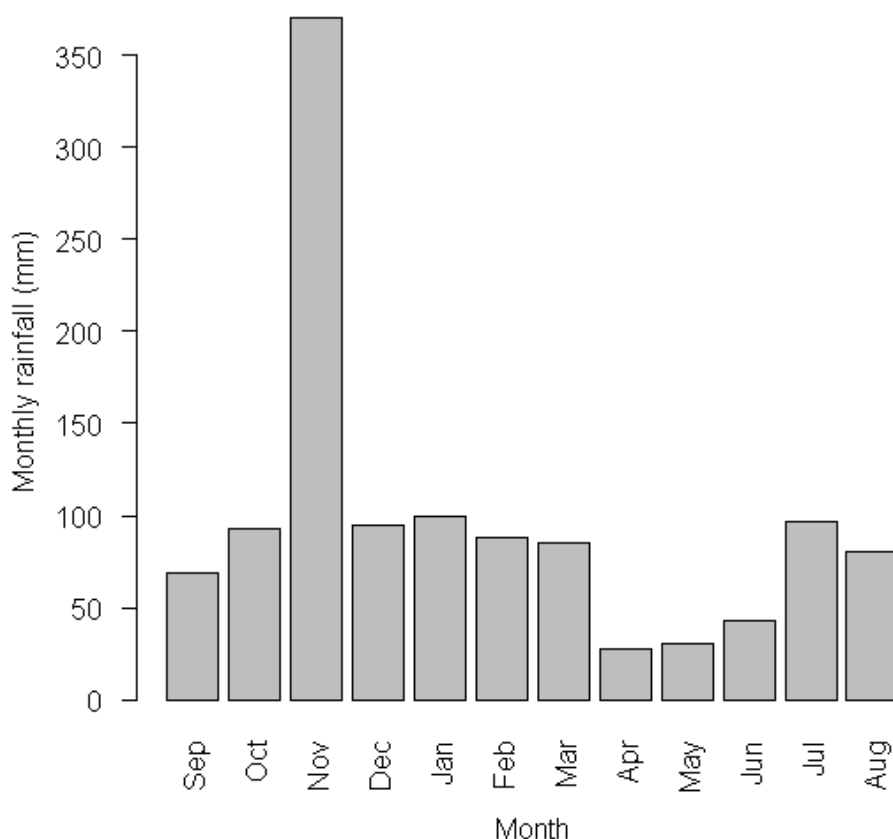


Figure 5.2. Total monthly rainfall data for September 2009 to August 2010 from the gauging station located in the village of Arncliffe, Littondale, Yorkshire Dales.

Sediment

The fine and coarse sediment used to fill the colonisation chambers were sharp sand and limestone chips respectively and both sediment types were limestone. This sediment is commonly available from builders merchants and similar to the geology (carboniferous limestone overlain with Gritstone) of the study site. The limestone chips and sharp sand were initially washed to remove possible contaminants. The fine sediment treatment contained only sharp sand and the coarse treatment only limestone gravel. The third treatment (m) contained approximately 50% sharp sand and 50% limestone gravel. The natural sediment treatment contained alluvial sediment excavated from the study site prior to insertion of the chambers. The alluvial sediment used in the control treatment was elutriated in a bucket and then rinsed using a portable pressure hose (Silverline[®] 2 litre pressure sprayer) to remove organic material and fauna, this was done over 0.5, 1 and 3mm stacked sieves.

Granulometry measurements of the sediment were conducted for each treatment following removal after each trial (Fig. 5.3). The sediment was initially air dried in a tray for one week regularly turning the sediment to ensure all moisture was removed, the sample was then weighed to the nearest gram (T_{sed}). The air dried sample was fed into a sediment shaker consisting of 9 sieves corresponding to the phi-scale -4 to 4. The sediment was shaken for 20 minutes and then each sieve sample weighed to the nearest gram (S_{sed}), giving a percentage of the total sediment mass ($S_{sed}/T_{sed} * 100$). The sediment fractions were then plotted on a cumulative frequency curve with the cumulative percentage of sediment passed through the sieves plotted against the phi scale (4 to -4) (Krumbein and Sloss, 1951).

Cumulative percentage weight of sediment passed through each sieve (phi scale -4 to 4) was calculated as:

$$\text{cumulative \% passed through sieve (i.e. phi scale -4)} = (S_{sed} / T_{sed}) \times 100$$

Sediment granulometry in the four treatments is shown in Figure 5.3. The fine and coarse treatments contained the highest and lowest proportions respectively of fine sediments. The intermediate and control treatments had similar slopes, both containing a mixture of fine and coarse sediments. The mixture and natural sediment treatment differed in their respective proportions of fine and coarse sediments. The mixture treatment contained a high proportion of fine sand (phi scale 2 and 1), conversely the natural sediment contained a high proportion of coarse sediments (phi scale -2 and -3).

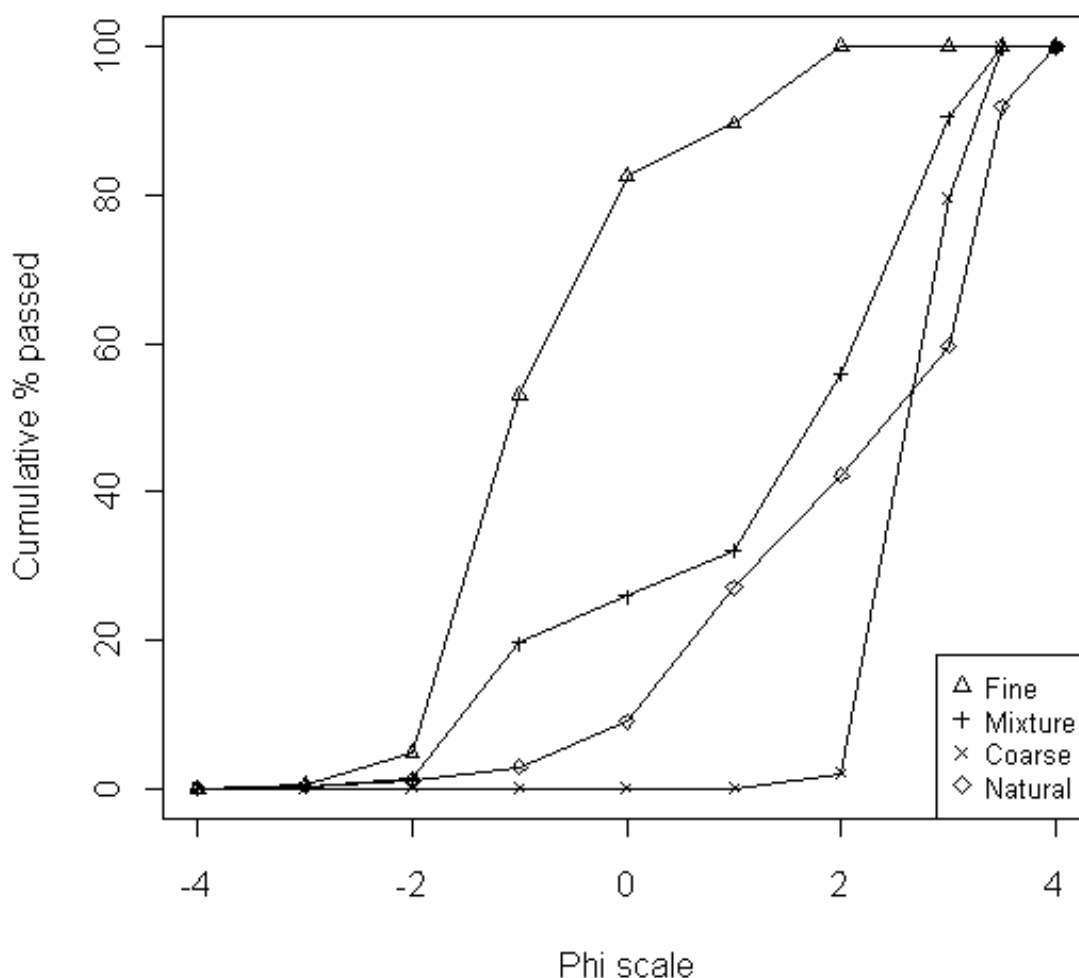


Figure 5.3. Plot of cumulative percentage frequency curves of the percentage weight of sediment passed through graded sieves (phi scale -4 to 4). The curves indicate the proportions of fine and coarse sediment present in each sediment treatment: fine treatment (100% sand); mixed treatment (50% sand – 50% gravel); coarse treatment (100% gravel); natural treatment (hyporheic sediment from study site).



Figure 5.4. Picture of colonisation chamber containing coarse sediment with lid removed. Yellow data logger is shown inserted in the pot. The tube inserted in the lid is for extracting water samples while in situ. Boulling silk (63 μ m mesh size) is visible on the end of the tube to prevent removal of taxa during water removal.

Water chemistry

Conductivity, dissolved oxygen and pH of both surface and hyporheic water were measured in the field. pH and conductivity were measured using a portable meter (pH - Hanna HI 9025[®]; conductivity - Hanna HI 9635[®]). Dissolved oxygen was determined using a Hach II portable colorimeter[®]; this method required 10ml of water which could be extracted from the pots minimising disturbance of the contents. The colorimeter uses a reagent which reacts with the oxygen in the sample allowing DO to be measured. Water samples were also extracted using the syringe for laboratory analysis of cations and anions using HPLC (Dionex, 2006). The water samples collected for HPLC analysis were frozen on the day of collection and later transported to the laboratory using a cool box.

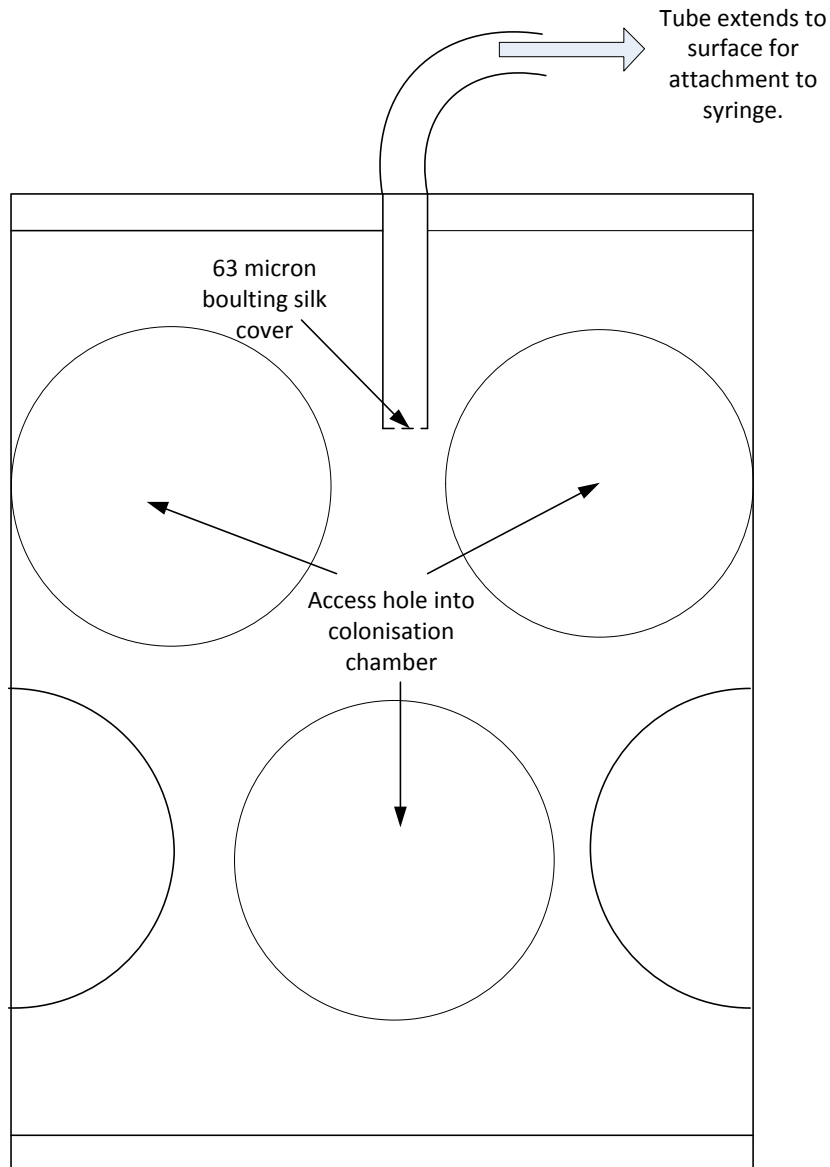


Figure 5.5. Side view of a colonisation chamber showing access holes from the side and insertion of sample tube into the top of chamber. The chambers are sealed at the top and bottom.

Surface and hyporheic water temperature readings were taken using Tinytag data loggers (Tinytag TG-4100[®]) with readings taken every 10 minutes. The data loggers were inserted into two chambers containing coarse sediments at the head of each riffle (Fig. 5:4). The coarse sediment treatments were chosen as water flow will be highest through the coarse sediments, reflecting the local hyporheic water temperature with a greater accuracy. The surface temperature was determined using one data logger placed at the head of the uppermost riffle. The data logger was inserted into a mesh bag with 1cm square mesh size,

allowing sufficient water flow through the mesh, the bag was then attached to the riverbed securely using a steel road pin. Rainfall data was available from a local weather station located in the nearby village of Arncliffe (Grid reference: 54° 8' 30" N 2° 6' 18" W; Elevation: 260m) providing met office data in real time.

Fauna and LOM

Insertion and removal of the chambers was done at low flow to minimise loss of sediment and fauna. The chamber design while inhibiting water flow through the top and bottom of the chambers also minimised the loss of biological material flushing out of the chamber upon removal. To extract the colonisation chambers sediment was removed from around the chamber, and then a plastic waterproof bag was placed tightly over the sides. The bag and chamber were then gripped firmly to minimise loss of material and extracted. The contents of the chamber and plastic bag were filtered over a 63 µm mesh size sieve. The contents of the sieve were bagged and preserved in 70% IMS for later sorting, enumeration and identification in the laboratory.

Sorting of samples in the laboratory involved rinsing of the sample over a 63 µm mesh size sieve, with the contents of the sieve then placed in a white flat bottomed tray. Elutriation of the sample in the tray was performed three times to separate the lighter organic material from the heavier sediments. The removed organic material was dispensed into a volumetric flask containing 800ml of water. The volumetric flask was agitated and a 20% subsample taken. To determine whether significant numbers of animals were lost during subsampling five random samples were 20% sub-sampled and processed. The remaining 80% of the sample was also processed to see how sub-sampling affected the overall explanatory power (Table 5.1). Sub-sampling accuracy was determined using the following formula:

$$\% \text{ error of sub-sample (x)} = [1 - (\text{sub-sample total} / \text{sample total})] \times 100$$

$$\% \text{ error of all sub-samples} = \sum \bar{x} / 5$$

Table 5:1. Results from subsampling of 5 randomly selected samples. Total abundance is given for a 20% sub-sample and for the remaining 80% of the sample. Total abundances are for each 1 litre volume colonisation chamber. Subsampling accuracy is given as a % error of estimate either +/- the actual abundance collected. Averaged subsample efficiency for the five samples is also given.

Random sample	Sub sample	Chironomid	Ostracod	Harpacticoid	Cyclopid	Macro invertebrate	Sub-sample accuracy (%)
Control	20%	15	2	4	2	3	-2.31
	80%	66	4	16	7	14	
Coarse	20%	12	0	2	0	2	+17.5
	80%	37	0	8	1	4	
Natural	20%	12	2	7	2	8	+12.25
	80%	43	5	20	6	31	
Mixed	20%	5	0	6	0	3	+5.71
	80%	20	1	24	0	7	
Fine	20%	6	1	5	1	1	+21.42
	80%	20	0	18	1	2	
Total sub-sampling accuracy (%)							+11.84

The samples were sorted using a Bogorov sorting tray under a Nikon DM-10 stereomicroscope. The fauna collected were identified to species level where possible. Oligochaetae, Diptera, Ostracoda and Nematoda were assigned to groups. The taxon-specific keys used for identification of fauna were: Copepoda (Einsle 1993, Janetzky et al. 1996); Cladocera (Scourfield 1994); Macroinvertebrates (Holland 1972, Elliott and Humpesch 1983, Hynes 1993, Wallace et al. 2003, Edington and Hildrew 2005) and Groundwater Crustacea (Gledhill 1993).

The length (l) and width (w) of all organisms (except Oligochaeta and nematodes due to preservation problems) were measured to the nearest micrometre using an image analyser and pre-taken photographs at calibrated exposures. If large groups of similar sized instars were found then 20% of the sample was measured to get a mean, the total number of individuals then counted and given the sub-sampled mean value. This process was primarily used for *Bryocamptus* sp. and Chironomidae larvae where abundances of the same instar were greater than 50. In order to estimate the volume of each species a prolate ellipsoid volume was calculated. Prolate ellipsoid volumes are a suitable measure for fauna found in

the hyporheic zone, where body width has been found to be more important than body length as depth increases into the sediments (Omesova et al. 2008). The prolate ellipsoid volume is calculated using the formulae:

$$V = 4/3\pi lw^2$$

where, w = width, l = length, V = volume (mm³)

After removal of organisms from the sample, the remaining material was dried at 40⁰C for 24 hours, weighed then ashed in a muffle furnace at 350⁰C for 4 hours to ascertain the loosely associated organic matter (LOM). LOM gives a rough approximation of the organic material associated with the sediment within each sample (Pusch and Schwoerbel 1994).

Statistical analyses

The predictors in this experiment were trial and sediment treatment. The responses tested were species abundance, water chemistry (Na, K Mg, Ca, Cl, NO₃, SO₂, LOM, pH, conductivity) and body size of fauna. All statistical analyses were performed with R version 2.11.12 (R Development Core Team, 2010). The effect of predictors on responses was tested in two main analyses: linear mixed effect model and analysis of covariance. Prior to analysis data exploration was conducted to identify possible outliers in the response and explanatory variables. Normality was checked using graphical plots, with deviations from normality corrected using log₁₀ (n+1) transformations if required. Residuals were plotted after model building to check for any violation of heterogeneity (Zuur et al. 2009). Comparisons of chemical and biological data between treatments and trials were performed using linear mixed effects (LME) models. The use of LME models accounted for the hierarchical nature of the experimental design, with treatments nested within riffles and riffles nested in trial. Mixed models allow for the use of both fixed and random effects in the study design. The following variables were fitted as fixed effects in the analyses: trial and treatment with riffle fitted as a random effect. The study design became unbalanced due to the loss of several

sediment treatments during the second trial, therefore restricted maximum likelihood method (REML) was used to estimate error terms. The model was chosen based on Akaike Information Criteria (AIC) scores, the score closest to zero being the model with the greatest parsimony. Data from both trials were merged based on the criteria that if no significant interactions occurred between treatment and trial then the treatment effect is the same in both trials. If there is a significant interaction then the trials cannot be combined. All interaction terms are included in the species and physico-chemical data tables for verification.

The model selection process begins by starting with a full model with all interactions and no random effect. This model was then compared to models containing a random intercept, a random intercept and slope and a random effects model. When a model is selected non-significant interactions are removed in a stepwise approach, starting with the full model including all interactions. After each model reduction the previous and current model were compared using analysis of variance (ANOVA). If the difference between the models is not significant then no explanatory power is lost in the reduced model, model reduction then continues until the difference between the models is significant and parsimony is reached (Zuur et al., 2009). Differences in body size were tested using analysis of covariance (ANCOVA), a multiple regression-based method. ANCOVA can compare two or more regression lines by testing the effect of a predictor (abundance) on the response variable (body size) while controlling for the effect of a continuous co-variable (treatment). The response variable is continuous with all measurements positive allowing a gamma or Gaussian distribution to be fitted to the data. Homogeneity of the regression slopes was tested, if the difference between slopes is not significant then the model is valid and the ANCOVA can proceed. No significant interaction between slopes indicates that the relationship between response variable and predictor are the same for all levels of the co-variable. If the slopes are the same then the rate of change is also the same, this allows the magnitude of the relationship to be tested by comparing the y-intercepts (body size).

Backward elimination of statistically non-significant factors was employed to obtain the optimum model. Post hoc tests were performed using the package “multcomp” version 1.2-5 (Bretz et al., 2010). Linear mixed effects models were performed using the package “nlme” version 3.1-102 (Pinheiro, 2011).

Table 5.2. Measured mean (± 1 SE) of physicochemistry of each treatment sampled in October and November 2009. LOM (loosely associated organic matter). Blank cells indicate variable below detection limit (1ppm) of HPLC equipment.

Variable	Treatments			
	Fine	Mixed	Coarse	Natural
October				
Na (mg L ⁻¹)	8.72 \pm 0.31	8.06 \pm 0.35	8.28 \pm 0.24	9.34 \pm 0.88
K (mg L ⁻¹)	<1ppm	<1ppm	<1ppm	<1ppm
Mg (mg L ⁻¹)	2.69 \pm 0.12	3.01 \pm 0.18	3.10 \pm 0.24	3.46 \pm 0.35
Ca (mg L ⁻¹)	32.62 \pm 2.72	39.36 \pm 3.36	39.67 \pm 2.26	35.45 \pm 3.11
Cl (mg L ⁻¹)	6.44 \pm 0.21	6.37 \pm 0.20	6.06 \pm 0.26	6.04 \pm 0.23
NO ₃ (mg L ⁻¹)	0.60 \pm 0.27	1.12 \pm 0.47	1.24 \pm 0.47	1.35 \pm 0.36
SO ₂ (mg L ⁻¹)	4.40 \pm 0.24	4.62 \pm 0.27	4.65 \pm 0.34	4.77 \pm 0.31
LOM (grams L ⁻¹)	0.04 \pm 0.01	0.05 \pm 0.01	0.10 \pm 0.01	0.13 \pm 0.02
DO (mg L ⁻¹)	8.53 \pm 0.38	8.81 \pm 0.05	9.86 \pm 0.27	9.17 \pm 0.33
pH	7.91 \pm 0.05	7.86 \pm 0.09	7.97 \pm 0.05	7.92 \pm 0.04
Cond (μ S cm ⁻¹)	284 \pm 2	286 \pm 1	284 \pm 1	282 \pm 1
November				
Variable	Fine	Mixed	Coarse	Natural
Na (mg L ⁻¹)	7.30 \pm 0.05	5.90 \pm 0.04	1.25 \pm 0.04	1.55 \pm 0.05
K (mg L ⁻¹)	<1ppm	<1ppm	<1ppm	<1ppm
Mg (mg L ⁻¹)	1.33 \pm 0.03	1.32 \pm 0.04	1.25 \pm 0.15	1.20 \pm 0.15
Ca (mg L ⁻¹)	46.84 \pm 1.64	38.53 \pm 0.77	51.59 \pm 1.95	56.73 \pm 1.39
Cl (mg L ⁻¹)	6.86 \pm 0.18	7.21 \pm 0.08	7.30 \pm 0.08	7.16 \pm 0.09
NO ₃ (mg L ⁻¹)	<1ppm	<1ppm	<1ppm	<1ppm
SO ₂ (mg L ⁻¹)	3.12 \pm 0.09	3.29 \pm 0.04	3.30 \pm 0.06	3.20 \pm 0.04
LOM (grams)	0.06 \pm 0.01	0.04 \pm 0.00	0.09 \pm 0.02	0.06 \pm 0.01
DO (mg L ⁻¹)	10.61 \pm 0.08	10.55 \pm 0.09	10.26 \pm 0.24	10.74 \pm 0.10
pH	7.81 \pm 0.03	7.84 \pm 0.05	7.89 \pm 0.04	7.87 \pm 0.03
Cond (μ S cm ⁻¹)	277 \pm 1	276 \pm 1	275 \pm 1	275 \pm 1

Results

Physicochemistry in the hyporheic zone across different sediment compositions

Both trials (October and November) showed similar physicochemistry. Water temperature in the HZ was similar to water temperature in the surfacewater. The pH was above neutral (7.86 - 7.97) and consistent for the area (Table 5:2). Dissolved ions were dominated by sodium,

magnesium, calcium and chloride (Table 5:2). Electrical conductivity varied slightly between trials with a slight reduction on trial 2 (Table 5:2). Nitrate and potassium were just on the border of detection limits for the HPLC equipment (minimum detection limit 1ppm) with many sites below 1ppm (Table 5:2). Although rainfall was very high in October this did not influence physicochemistry markedly (Table 5:2). Although surface water temperature differed markedly between trials, the temperature in the HZ did not (Fig 5:6).

Influence of trial and granulometry on physicochemistry and LOM

There were no significant interactions between trial and sediment treatments for all physicochemical parameters apart from LOM and calcium (Table 5:3). Calcium levels were higher during the second trial in the coarse, natural and fine sediment treatments. Calcium did not differ significantly between trials in the fine sediment treatments (Table 5:3). LOM was significantly lower during the second trial in the mixed, coarse and natural treatments and significantly higher in the fine treatment although LOM was still low during both trials in the fine treatment (Table 5:3).

LOM and calcium differed significantly between treatments but all other physicochemical variables (Na, Mg, Cl, NO₃, SO₄, DO, pH and electrical conductivity) did not (Table 5:3). In the first trial LOM was found to be significantly lower in the treatments containing fine sand (fine and mixed) compared to the coarse and natural treatments containing a higher proportion of coarse sediment (Table 5:4; Fig 5.7). In the second trial calcium was significantly lower in the mixed treatments compared to the fine and coarse treatment, with calcium in the natural treatment significantly higher than in all other treatments (Table 5:3). Significant differences were found between physicochemical variables between the two trials (Table 5:3). LOM, sodium, magnesium and sulphate were significantly higher during the second trial, whereas calcium and chloride were both significantly lower during the second trial (Table 5:3). Three variables (pH, DO and NO₃) showed no significant difference between trials (Table 5:3).

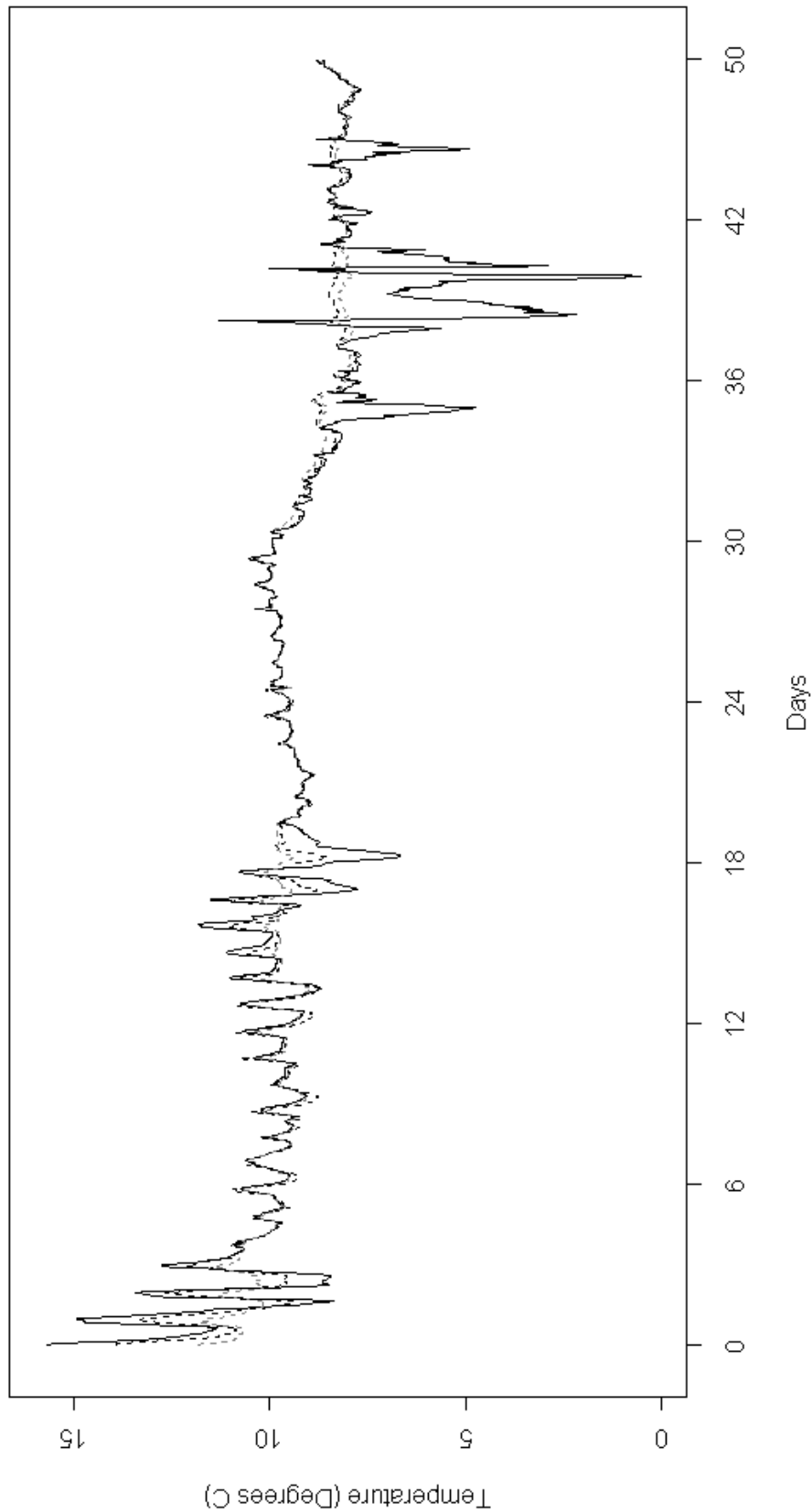


Figure 5.6. Temperature data collected from the surface and hyporheic zone of the River Skirfare. Temperature readings were taken every 30 minutes from 16:45 on the 29/09/2009. Solid line = surface temp, black dashed line = mean riffle 1, grey dashed line = mean riffle 2, data from riffle 3 not available for whole study due to lost data logger.

Table 5.3 Results of Linear mixed effects model of comparisons of physicochemistry across treatments and trials. Only data for treatment effects that showed significant results are shown. There was a significant interaction between trial and treatment for both calcium and LOM therefore results are given separately for trial 1 and 2.

Variable	Comparison	df	F-value	p-value
LOM	Trial	1,70	4.214	0.044
	Treatment	3,70	10.299	<0.001
	Trial x treatment	3,70	3.211	0.028
Calcium	Trial	1,70	69.648	<0.001
	Treatment	3,70	4.112	0.009
	Trial x treatment	3,70	8.134	<0.001
LOM trial1	Treatment	3,42	11.8	<0.001
LOM trial 2	Treatment	3,27	0.61	0.54
Calcium trial 1	Treatment	3,42	2.27	0.09
Calcium trial 2	Treatment	3,27	17.81	<0.001
Sodium	Trial	1,70	490.192	<0.001
	Treatment	3,70	1.169	0.327
	Trial x treatment	3,70	0.797	0.499
Magnesium	Trial	1,70	128.335	<0.001
	Treatment	3,70	1.218	0.309
	Trial x treatment	3,70	1.467	0.231
Chloride	Trial	1,70	30.928	<0.001
	Treatment	3,70	0.405	0.750
	Trial x treatment	3,70	1.541	0.211
Nitrate	Trial	1,70	14.034	0.040
	Treatment	3,70	1.096	0.356
	Trial x treatment	1,70	0.192	0.901
Sulphate	Trial	1,70	69.984	<0.001
	Treatment	3,70	0.552	0.648
	Trial x treatment	3,70	0.166	0.919
Dissolved oxygen	Trial	1,70	34.447	<0.001
	Treatment	3,70	1.525	0.215
	Trial x treatment	3,70	2.239	0.091
pH	Trial	1,70	3.470	0.067
	Treatment	3,70	0.950	0.423
	Trial x treatment	3,70	0.210	0.888
Electrical conductivity	Trial	1,70	68.860	<0.001
	Treatment	3,70	1.730	0.168
	Trial x treatment	1,70	0.610	0.608

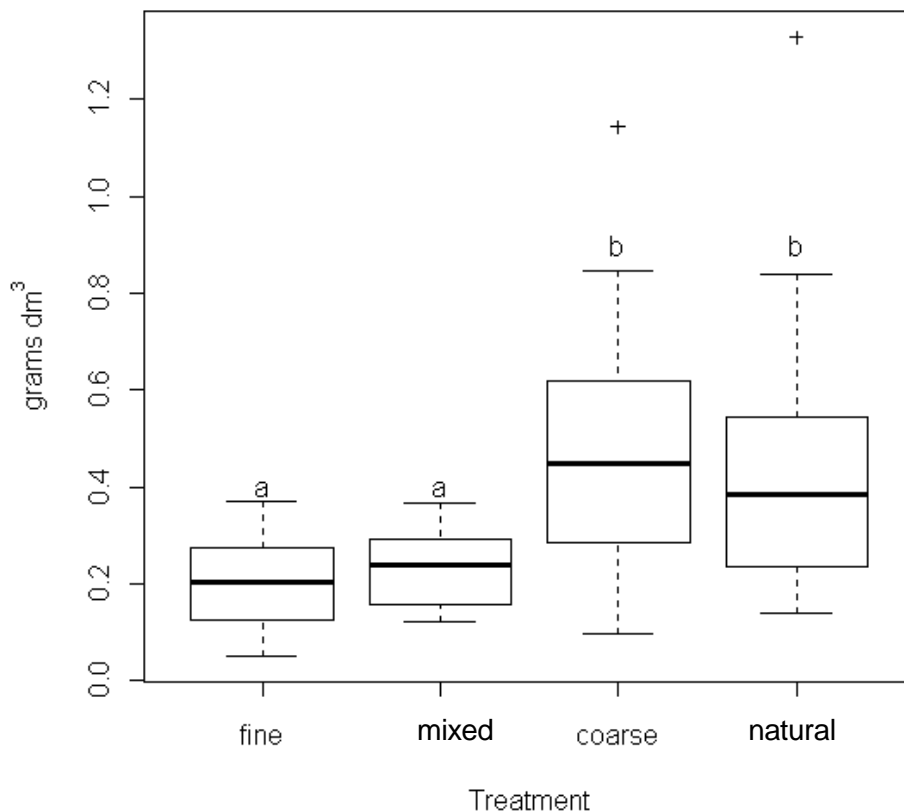


Figure 5.7. Boxplot of LOM collected from each treatment during the October trial. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Boxplots with the same letter indicate no significant difference between treatments.

Table 5.4. Results from TUKEY multiple comparison post-hoc tests of differences between sediment treatments of LOM from trial 1. Symbols indicate: (f = fine, m = mixed, c = coarse, n = natural sediment)

Treatment	f-m	f-c	f-n	m-c	m-n	c-n
LOM	0.994	<0.001	0.003	<0.001	0.001	0.967

Species collected

In total 53 species and higher taxa colonised the chambers in both experimental trials. This included twenty-two Crustacea with fourteen identified to species, seven to genus and Ostracoda identified to class (Appendix 4). The Crustacea were dominated by three species of Harpacticoida, *Bryocamptus zschokkei*, *B. minutus* and *B. echinatus*, and two Cyclopoida

genera *Acanthocyclops* sp. and *Diacyclops* sp. One stygobite crustacean, *Parastenocaris* sp. was recorded along with a number of species associated with springs and seeps (*Bryocamptus echinatus*, *Bryocamptus cuspidatus*, *Canthocamptus staphylinus*, *Moraria* sp.) (Sarkka et al. 1998). Twenty-four Insecta also colonised the chambers with twelve identified to species and nine to genus. Chironomidae were identified to family level due to the prevalence of early instar larvae. Chironomidae larvae dominated the Insecta group along with three species of macroinvertebrates (*Chloroperla tripunctata*, *Leuctra* sp. and *Esolus parallelolidus*). Four species of Collembola also colonised the chambers (Appendix 4) during both trials. Chydoridae also colonised the chambers during the October study and were dominated by one species *Alona affinis* (Appendix 4).

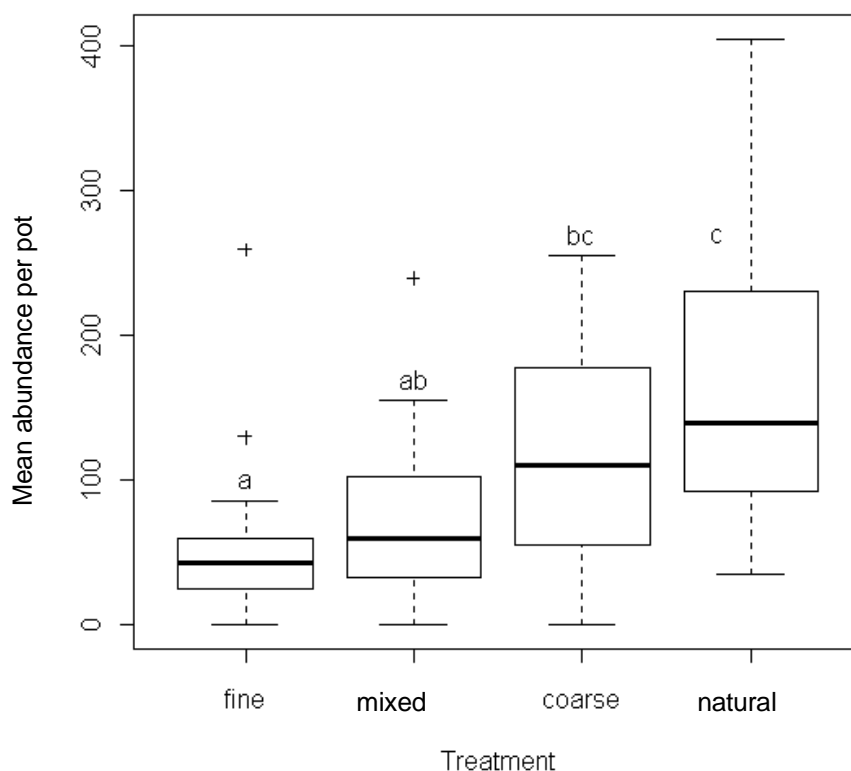


Figure 5.8. Boxplots of Chironomidae abundance across sediment treatments. Boxplots with the same letter indicate no significant difference between treatments. Data is presented from the October and November trials. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range.

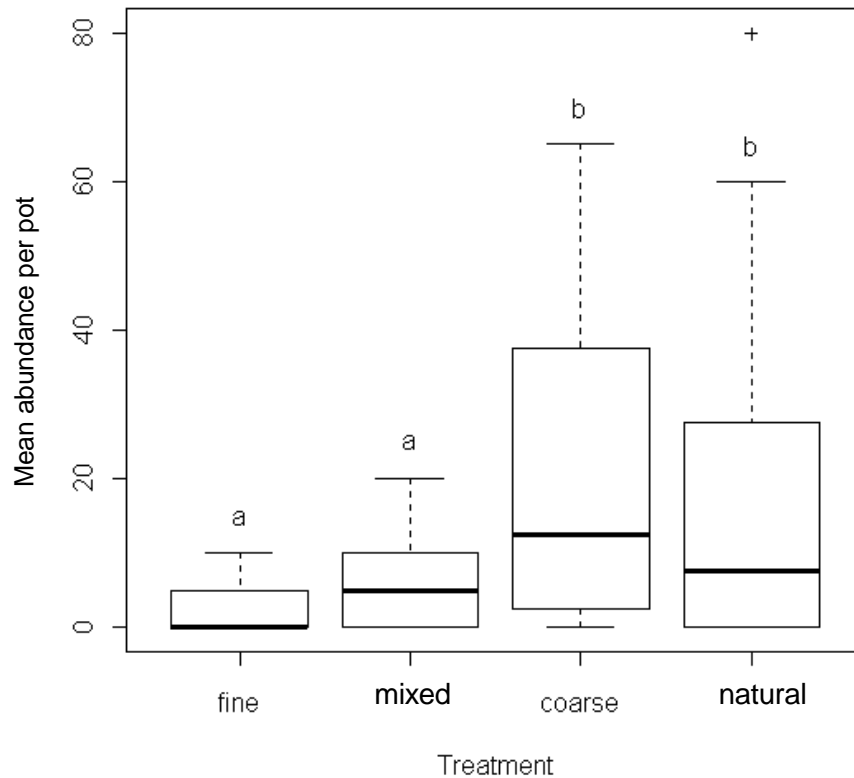


Figure 5.9. Boxplots of *C. tripunctata* abundance across sediment treatments. Boxplots with the same letter indicate no significant difference between treatments. Data presented is from the October and November trials. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range.

Influence of trial and granulometry on faunal abundance

There were no significant interactions between trial and treatment for all groups of meio- and macrofauna, this indicated that although abundance decreased during the second visit, the relative abundance patterns within treatments were the same in both experimental trials (Table 5:5). Chironomidae abundance was significantly higher in the natural treatments in comparison to the fine and mixed treatment and also significantly higher in the coarse treatment in comparison to the fine treatment (Table 5:6; Fig. 5:8). The abundance of Acari was significantly higher in the natural treatment in comparison to the fine treatment (Table 5:6). There was no significant difference in abundance of Cyclopoida (*Diacyclops* sp. and *Acanthocyclops* sp.), Harpacticoida (*B. zschokkei*, *B. minutus*, and *B. echinatus*), Oligochaeta, Collembola and the chydorid *Alona affinis* between treatments (Table 5:5). The

abundance of Harpacticoida (*B. zschokkei*, *B. minutus*), Cyclopoida (*Diacyclops* sp. and *Acanthocyclops* sp.), Chironomidae, Acari and the chydorid cladoceran *Alona affinis* was significantly lower during the second trial (Table 5:5). Oligochaeta, Collembola and *B. echinatus* abundance did not differ significantly between trials.

Table 5.5 Linear mixed effects model results of comparisons of abundances of major taxonomic groups across treatments and trials. Three-way interactions are omitted as not significant (a = adult, j = juvenile).

Taxa	Comparison	df	F-value	p-value
Chironomidae	Trial	1,70	50.781	<0.001
	Treatment	3,70	8.795	<0.001
	Trial x treatment	3,70	0.597	0.619
Harpacticoida	Trial	1,70	32.009	<0.001
	Treatment	3,70	2.036	0.117
	Trial x treatment	3,70	0.347	0.791
<i>B.zschokkei</i>	Trial	1,70	28.017	<0.001
	Treatment	3,70	1.346	0.266
	Trial x treatment	3,70	0.316	0.814
<i>B.minutus</i>	Trial	1,70	19.705	<0.001
	Treatment	3,70	0.952	0.420
	Trial x treatment	3,70	0.884	0.454
<i>B.echinatus</i>	Trial	1,70	0.043	0.835
	Treatment	3,70	0.477	0.699
	Trial x treatment	3,70	1.177	0.325
Cyclopoida	Trial	1,70	14.806	<0.001
	Treatment	3,70	2.560	0.061
	Trial x treatment	3,70	2.857	0.043
<i>C. tripunctata</i>	Trial	1,70	1.816	0.181
	Treatment	3,70	24.879	<0.001
	Trial x treatment	3,70	0.301	0.585
<i>Leuctra</i> sp.	Trial	1,70	0.884	0.350
	Treatment	3,70	1.364	0.260
	Trial x treatment	3,70	1.477	0.228
<i>E. parallelopidus</i> j	Trial	1,70	0.610	0.437
	Treatment	3,70	0.118	0.949
	Trial x treatment	3,70	2.626	0.057
<i>E. parallelopidus</i> a	Trial	1,70	0.370	0.544
	Treatment	3,70	3.721	0.015
	Trial x treatment	3,70	0.154	0.927
Acari	Trial	1,70	8.838	0.004
	Treatment	3,70	3.223	0.027
	Trial x treatment	3,70	0.117	0.949
Oligochaeta	Trial	1,70	0.116	0.734
	Treatment	3,70	0.173	0.678
	Trial x treatment	3,70	0.544	0.463
<i>A. affinis</i>	Trial	1,70	36.218	<0.001
	Treatment	3,70	0.457	0.712
	Trial x treatment	3,70	1.321	0.274
Collembola	Trial	1,70	0.118	0.730
	Treatment	3,70	0.932	0.429
	Trial x treatment	3,70	0.175	0.911

Table 5.6. Results from TUKEY multiple comparison post-hoc tests of differences between sediment treatments for main fixed effects. Symbols indicate: (f=fine, m=mixed, c=coarse, n = natural). (l = larvae, a = adult).

Comparison	f-m	f-c	f-n	m-c	m-n	c-n
Chironomidae	0.504	0.016	<0.001	0.400	0.002	0.200
Harpacticoida	0.498	0.980	0.106	0.742	0.823	0.238
<i>B. zschokkei</i>	0.574	0.981	0.889	0.830	0.187	0.691
<i>B. minutus</i>	0.458	0.467	0.676	1.000	0.966	0.988
<i>B. echinatus</i>	0.868	0.941	0.646	0.997	0.978	0.933
Cyclopoida	0.933	0.346	0.492	0.109	0.185	0.995
<i>C. tripunctata</i>	0.188	<0.001	<0.001	0.002	0.142	0.479
<i>Leuctra</i> sp.	0.210	0.554	0.735	0.915	0.783	0.992
<i>E. paralellopidus</i> l	0.993	0.996	0.940	1.000	0.991	0.986
<i>E. paralellopidus</i> a	0.859	0.474	0.006	0.915	0.064	0.265
Acari	0.318	0.181	0.009	0.989	0.490	0.686
Oligochaeta	0.771	0.770	0.997	0.217	0.870	0.652
<i>A. affinis</i>	0.960	0.919	0.995	0.667	0.881	0.979

Macroinvertebrates were dominated by *Chloroperla tripunctata*, *Leuctra* sp. and *Esolus paralellopidus* (adult and larvae). The abundance of *C. tripunctata* was significantly higher in the coarse and natural treatments in comparison to the fine treatments (Table 5:6; Fig 5:9). Adult *E. paralellopidus* abundance was significantly higher in the natural treatment compared to the fine treatment (Table 5:6). Larvae of *Leuctra* sp. and *E. paralellopidus* showed no significant difference in abundance between treatments (Table 5:5). *Chloroperla tripunctata*, *Leuctra* sp. and *Esolus paralellopidus* (adult and larvae) abundance did not differ significantly between trials (Table 5:5).

Influence of trial and granulometry on faunal body size

Body size patterns across treatments varied within meio- and macrofauna size classes (Figure 5.10). The greatest variation in body size among sediment treatments occurred in the Chironomidae (Table 5:7; Fig 5:11). Chironomidae body size followed a stepwise pattern with body size lowest in the fine sediments and highest in the coarse and natural sediments (Fig 5:11). Cyclopoida body size was significantly greater in the mixed, coarse and natural treatments compared with the fine treatment (Table 5:7). Harpacticoida and Chydoridae (A.

affinis) showed no significant difference in body size between sediment treatments (Table 5:7). Body size in the dominant macroinvertebrate species *C. trispinosa* was significantly smaller in the fine compared to the coarse sediment treatment (Table 5.7)

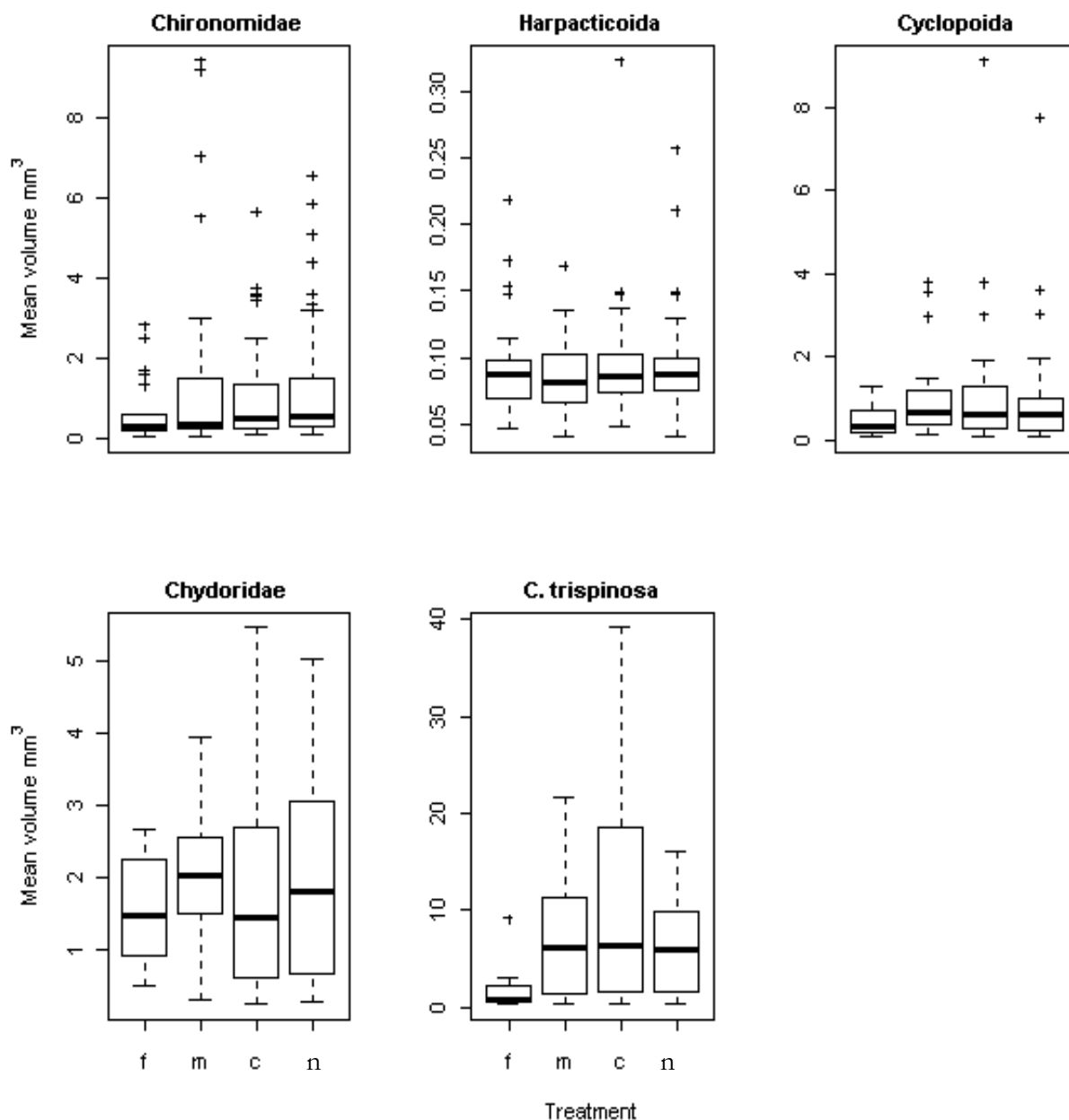


Figure 5.10. Body size (mm^3) of meio- and macroinvertebrate fauna collected from colonisation treatments. Only data from the dominant taxonomic groups are presented. The central line in each box is the median residual (50th percentile), and the limits of each box match the 25th and 75th quartiles of the distribution. Modified boxplots are displayed to highlight outliers. Minimum and maximum values excluding outliers are indicated by the error bars with distance calculated as 1.5 times the interquartile range. Key: f = fine sediment, m = mixed sediment, c = coarse sediment, n = natural sediment.

Table 5.7. ANCOVA for the relationship between body size (dependent) and abundance (predictor) between treatments (co-variate). The intercept for the fine treatment is the baseline level with the intercept estimates positive and negative around the baseline level

	Comparison	y-intercept	Std.error	df	t-value	P-value
Chironomidae	Fine (Intercept)	-0.005	0.090	3,162	-0.055	
	slope	-0.641	0.069	3,162	-9.237	<0.001***
	Mixed	0.169	0.098	3,162	1.721	0.087
	Coarse	0.299	0.098	3,162	3.045	0.003**
	Natural	0.411	0.097	3,162	4.242	<0.001***
<i>C. trispinosa</i>	Fine (Intercept)	0.339	0.186	3,63	1.826	
	slope	0.136	0.289	3,63	0.471	0.639
	Mixed	0.369	0.201	3,63	1.842	0.070.
	Coarse	0.459	0.202	3,63	2.284	0.025*
	Natural	0.318	0.205	3,63	1.554	0.125
Harpacticoida	Fine (Intercept)	-1.089	0.029	3,150	-37.175	
	slope	0.049	0.031	3,150	1.604	0.111
	Mixed	-0.019	0.033	3,150	-0.585	0.559
	Coarse	0.013	0.033	3,150	0.399	0.690
	Natural	0.018	0.032	3,150	0.570	0.570
Cyclopoida	Fine (Intercept)	-0.424	0.104	3,102	-4.070	
	slope	-0.325	0.170	3,102	-1.913	0.058.
	Mixed	0.302	0.137	3,102	2.201	0.030*
	Coarse	0.354	0.132	3,102	2.680	0.009**
	Natural	0.255	0.126	3,102	2.029	0.045*
<i>A. affinis</i>	Fine (Intercept)	0.116	0.116	3,47	0.998	
	slope	0.075	0.221	3,47	0.342	0.734
	Mixed	0.104	0.160	3,47	0.652	0.518
	Coarse	-0.050	0.155	3,47	-0.327	0.745
	Natural	0.009	0.152	3,47	0.057	0.955

Discussion

Hydrological effects influence the size, shape, hydraulic conductivity, permeability and sorting of riverbed sediments (Newbury 1984). The size (i.e. coarse and fine) of riverbed sediments and relative proportions of coarse and fine grained material is related to the dominant local geology (Valett et al. 1997), with interstitial spaces within the sediment matrix increasing as the proportion of coarse sediment increases. The ability to colonise sediments is therefore driven by numerous factors: (1) the ability to access the sediments (i.e. small body size, worm like shape, burrowing ability, interstitial space) (Strayer et al. 1997, Hakenkamp and Morin 2000), (2) availability of energy within the sediments (FPOM,

CPOM, temperature (ectotherms) (Navel et al. 2010b), tolerance to low DO (i.e. low DO in fine sediment) (Malard and Hervant 1999, Olsen and Townsend 2003) and (4) tolerance of low pH (Rundle 1990, Schindler and Krabbenhoft 1998, Datry et al. 2008).

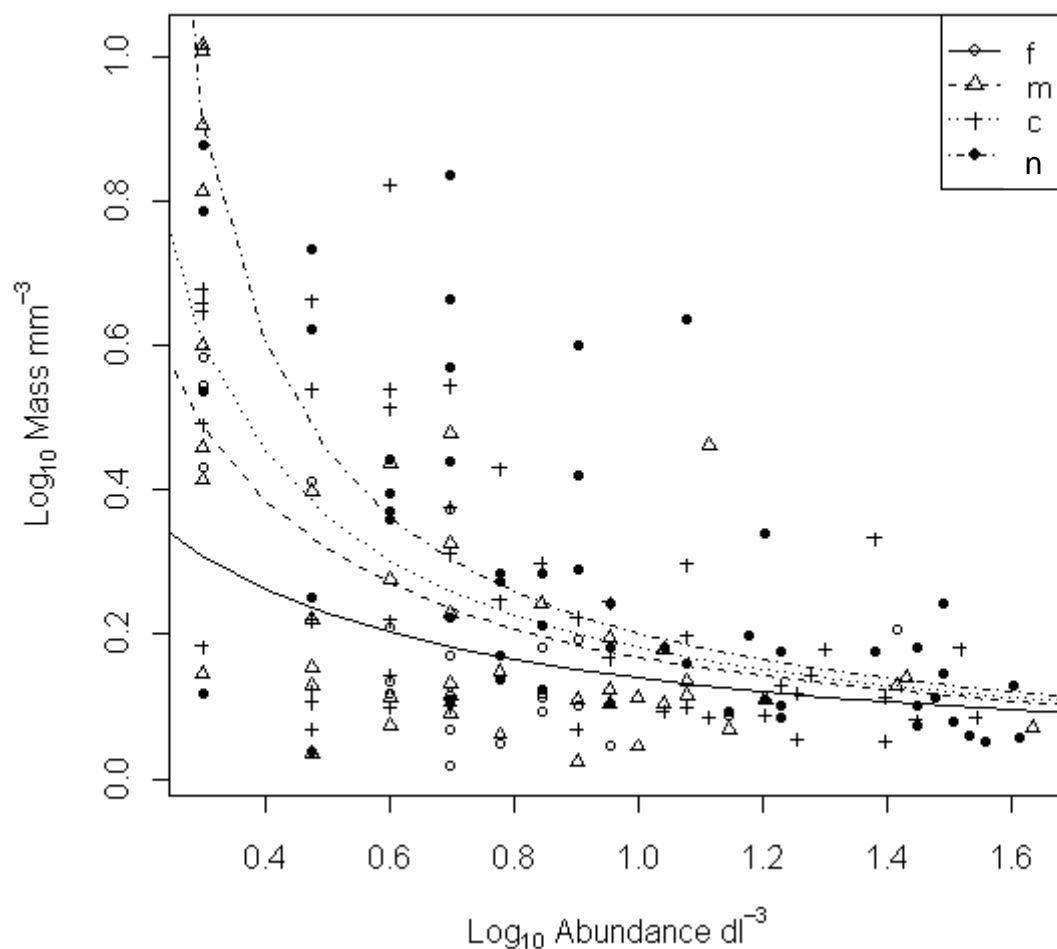


Figure 5.11. Plot of ANCOVA results of Chironomidae body size abundance slopes across sediment treatments. Symbols indicate: (f=fine, m=mixed, c=coarse, n = natural)

Physicochemical effects of granulometry

Physicochemistry (except LOM and calcium) was similar across all sediment treatments with the influence of sediment size having minimal effect on physicochemistry in this study. My results did not support the hypothesis i.e. an increase in sediment size would increase dissolved oxygen and decrease dissolved mineral concentrations. These results suggest the hyporheic zone (30cm depth) of this karst system is well connected with the surface water with uptake of DO not exceeding replenishment. Similarly, no differences in dissolved

minerals were observed, suggesting high connectivity within both the hyporheic zone and treatments, with water chemistry therefore at similar concentrations within the hyporheic zone and treatments. Temperature data also indicated high connectivity between surfacewater and the hyporheic zone at low flow. There was evidence of attenuation of high and low surfacewater temperature peaks in the hyporheic zone, with variability of hyporheic water temperature low relative to surface water. Studies have shown diel temperature fluctuations decrease rapidly as vertical depth increases (Tonolla et al. 2010) with fluctuations increasing with depth where connectivity is high (coarse sediments) (Lapham 1989).

The significant reduction in LOM in the fine and mixed treatments compared to the coarse and natural treatments in trial 1 supported my hypothesis i.e. LOM will be higher in sediments containing a high proportion of coarse material. When interstitial space becomes small, sediments can act like a filter preventing inputs of CPOM into the fine sediment layers. Breakdown of CPOM by shredders into FPOM will allow organic material to penetrate the sediment interstices of the hyporheic zone (Schalchli 1992, Vervier et al. 1992, Joyce and Wotton 2008). Conversely, the ability of the hyporheic zone to retain CPOM deposited during flood events can provide a source of DOC to biofilms (Crenshaw et al. 2002). In this study the effect of the flood event resulted in a decrease of LOM during the second trial in all treatments apart from the fine sediment. The fine sediment treatment had a small but significant increase in LOM during the second trial, this may be due to organic matter being flushed out of the coarse sediments but retained by the fine sediments. Studies have shown sediments exhibiting low hydraulic conductivities (fine sediment) become less permeable over time due to the retention of more fine sediment particles. Conversely, sediments exhibiting high hydraulic conductivities (coarse sediments) will become more permeable as sediment flushing will occur (Nowinski et al. 2011).

Influence of sediment on meiofauna

The diversity and density of meiofauna in the hyporheic zone can be extremely high (Palmer, 1991), although studies have shown physical habitat properties can have a strong influence on larval copepods and chironomids (Nogaro et al. 2008, Schmid and Schmid-Araya 2010).. The hyporheic zone is inherently patchy containing areas of both fine and coarse sediments (Swan and Palmer 2000, Olsen and Townsend 2003). Fauna can exploit different sediment compositions dependent on their relative body size and burrowing ability (Strayer et al. 1997, Hakenkamp and Morin 2000). An organism's morphology, physiology and behaviour will limit how accessible and hospitable interstitial spaces will be, and meiofauna are predicted to have the greatest influence on stream ecosystem processes in fine sediments (Hakenkamp and Morin 2000). My results broadly support my hypothesis i.e. that meiofauna abundance will be high across sediment treatments, though differences in the abundance of Chironomidae were found.

In this study Chironomidae abundance was significantly higher in the coarse sediment treatment. However, abundance was still high relative to other taxa in the fine sediment treatments, in agreement with other studies which found Chironomidae abundant across a range of sediment sizes (Ruse 1994). The higher abundance of Chironomidae in the coarse sediment matched the larger quantities of LOM in this treatment, suggesting where LOM is available Chironomidae will be more abundant. The feeding patterns of Chironomidae are various with *Chironomus* sp. and *Polypedulum* sp. feeding predominately on detritus (Titmus and Badcock 1981). Also the growth rate of later instar *Chironomus* sp. has been linked with high food quality i.e. CPOM which would be more abundant in the coarse treatments (De Haas et al. 2006). Chironomidae larvae can be found both at the sediment surface and in the hyporheic zone (Hunt and Stanley 2003). Chironomidae larvae build silk tubes in the sediment and collect particles from the tube entrance for feeding and tube construction (Mermillod-Blondin et al. 2002). Sedentary feeders such as Chironomidae larvae will require

water flow to provide an input of organic material to collect for feeding (Lencioni and Rossaro 2005), also a possible reason for the increase in abundance of Chironomidae in the coarse treatment.

Numerous studies have found copepod abundance to be strongly affected by granulometry and hydraulic conductivity at large (Shiozawa 1991, Fiasca et al. 2005, Robertson and Milner 2006, Dole-Olivier et al. 2009b) and small (Schmid and Schmid-Araya 2010) spatial scales. In this study, copepods were ubiquitous across all treatments and granulometry had little effect on colonisation patterns. The high abundance of the harpacticoid copepods *B. zschokkei*, *B. minutus* and *B. echinatus* and the cyclopoid copepods *Diacyclops* sp. and *Acanthocyclops* sp in the River Skirfare is consistent with results found in similar systems (Sarkka et al. 1998, Sarkka and Makela 1999, Lewis and Reid 2007, Galassi et al. 2009a). Harpacticoida and Cyclopoida have been described by Galassi et al. (2009a: p. 696) as the “Groundwater copepods *par excellence*” and dominate the benthos in many streams and rivers (Dole-Olivier et al. 2000).

A number of other taxa occupying the meiofaunal size class also colonised the chambers, these included Collembola and Chydoridae and were common across all sediment treatments with no significant differences in abundance. Chydoridae of the sub-family Aloninae, are known to colonise hyporheic sediments (Brancelj and Dumont 2007, Van Damme et al. 2009). The size, shape and mode of locomotion make *Alona* species successful colonizers of the hyporheic habitat (Brancelj and Dumont 2007). The high abundance of Chydoridae (*Alona affinis*) is consistent with results from other studies on slow flowing rivers (Robertson 1990, 1995). Karst rivers by their nature of being highly dynamic can move from a high flow state to a low flow state relatively quickly (Bonacci et al. 2009), with the coarse substrate providing refugia for Cladocera and Calanoida (Brancelj and Dumont 2007).

Influence of sediment on macrofauna

Macrofaunal abundance was significantly higher in the coarse sediments, specifically amongst three families the Chloroperlidae, Leuctridae and Elmidae all of which are common inhabitants of the hyporheic zone (Malard et al. 2003b, Storey and Williams 2004, Datry et al. 2007, Silveri et al. 2008). These results support my hypothesis that increased interstitial space (coarse sediments) will result in higher abundances of macroinvertebrate fauna. Chloroperlidae are primarily predators (Stewart and Harper 1996) with the high abundances found in the coarse and control treatments suggesting that *C. tripunctata* is limited by sediment size to areas available for colonisation and feeding. Similarly adults of *E. parallelipidus* were low in abundance in the fine sediment treatment with abundance increasing as sediment size increased. Elmidae are predominately collector-gatherers and scrapers feeding on periphyton and detritus (Elliott 2008). The higher concentrations of LOM in the coarse and natural treatments may attract Chironomidae and larger scrapers/detritivores which in turn may attract larger predators in particular Chloroperlidae.

The influence of sediment size on a range of meio- and macrofauna has been clearly demonstrated in this study. Smaller meiofauna are ubiquitous across all sediment sizes, whereas larger macrofauna are less abundant in the fine sediments. Geology affects the hyporheic zone directly, being the primary source of alluvial deposits in rivers and streams. Limestone deposits are characteristically large, providing interstitial space available to a large range of macro- and meiofauna (Galassi et al. 2009a, Martin et al. 2009). The large pore spaces also allow the movement of LOM and DO into sediments providing the necessary basal resources for meio- and macrofauna to thrive (Pusch et al. 1998). In comparison, geological formations such as chalk and clay provide very fine alluvial sediments that are accessible to only the smallest taxa. Inputs of organic matter into these sediments are limited to the surface layers restricting productivity in the deeper hyporheic zone (Pretty et al. 2006).

Body size patterns across sediment patch types

Meiofauna

Chironomidae larvae occupying the macrofaunal size class were found predominately in the mixed, coarse and natural treatments, whereas meiofaunal sized Chironomidae were found across all sediment treatments and dominant in the fine sediment treatment. The increase in body size of Chironomidae as sediment size increased is consistent with other studies (Vos et al. 2002, Rae 2004), with Chironomidae found to actively seek higher quality food as their growth proceeds (De Haas et al. 2006). In this study, larger bodied Chironomidae seem to be colonising sediments containing more LOM. Studies have shown instar III *Chironomus riparius* larvae will disperse when density becomes too high, while instar III larvae will also deter colonisation by instar I larvae through competition (Silver et al. 2004). Congeneric Chironomidae instars have also been shown to partition streambed resources when conditions allow (Silver et al. 2004), possibly explaining the increase in body size as sediment size increased. In fine sediments, FPOM and biofilms low in nutrients will be dominant with nutritious CPOM abundant in coarse sediments (Storey et al. 1999, Arnon et al. 2010). Energy flow and nutrient dynamics in the hyporheic zone has been linked to the quantity and quality of carbon input, particularly the influx of CPOM (Boulton and Foster 1998, Crenshaw et al. 2002). Body size of Harpacticoida was similar across all sediment treatments during both trials. Harpacticoida can access the interstitial spaces of sediment particle sizes between 160-170 μm (phi scale 2-3) (McLachlan and Brown 2006). The smallest sediment particle size in this study (phi scale 4) contributed <20% of the sediment composition in the fine and intermediate sediment treatments, therefore interstitial space is sufficient for colonisation by small meiofaunal groups.

Macrofauna

The interstitial spaces of benthic sediments are known to be inhabited by macroinvertebrate fauna particularly in the upper sediment layers (Marchant 1995, Weigelhofer and Waringer

2003a, Bo et al. 2006), where flushing removes fine sediment (Chen 2011, Nowinski et al. 2011) and invertebrate activities expand pore spaces (Song et al. 2007). Macroinvertebrate nymphal development can be reduced in fine sediments and increased in coarse sediments for both Nemouridae (Plecoptera) (Franken et al. 2008) and Gammaridae (Amphipoda) (Franken et al. 2006). The results from this study support the hypothesis i.e. that an increase the proportion of coarse sediment (larger interstitial space) will result in the body size of macroinvertebrates increasing. The body size of *C. tripunctata* was significantly smaller in the fine treatment in comparison to the coarse treatment. Larger bodied *C. tripunctata* were low in abundance in the fine treatment suggesting that fine sediments are inaccessible and/or inhospitable. The data from this study suggests that interstitial space, LOM and body size/abundance of Chironomidae larvae were the factors that differentiated the fine from the coarse sediment treatments. Numerous studies have shown the abundance and diversity of benthic invertebrate's decreases with depth (Weigelhofer and Waringer 2003a, Storey and Dudley-Williams 2004, Varricchione et al. 2005).

Conclusion

In conclusion, this study supports the hypothesis that coarse sediments provide more interstitial space and greater hydraulic conductivity which supports a diverse meio- and macrofaunal invertebrate assemblage. Meiofauna (copepods and early instar Chironomidae) become increasingly important as sediment size decreases, as their relative abundance to macrofauna is proportionally higher in the fine sediments. The increase in body size and abundance of Chironomidae in the coarse sediment treatments was associated with an increase in LOM. Macrofaunal sized Chironomidae have a higher nutritional requirement than smaller individuals and consequently sediment containing higher amounts of LOM may be preferable. Species abundance and body size was highest in treatments containing the greatest proportion of coarse sediment and also LOM. These results highlight the importance of coarse sediment composition supporting the hyporheic community assemblage.

Deleterious influences on sediments primarily through the input of fine sediments from agricultural run-off can quickly impact the meiofaunal community inhabiting the naturally occurring fine sediments in the hyporheic zone.

Chapter VI: Discussion

Introduction

Physical hydrogeological conditions are vitally important in the hyporheic zone controlling the influx and efflux of dissolved oxygen, nutrients and minerals and importantly accessibility of the hyporheic zone for epigeal and hypogean fauna. Hydrogeology describes the distribution, movement and geological interaction of water in the Earth's crust. A more holistic view of hydrogeology incorporates hydrology and interactions between surfacewater and groundwater which key ecosystem processes (e.g. nutrient cycling, production and fluxes of nutrients and energy). Therefore, hydrogeology has a major influence on hyporheic faunal assemblages and the linking of organisms with their environment. Thus, if hydrogeology can regulate ecosystem processes then characteristic faunal assemblages will be indicative of specific hydrogeological properties. One key fundamental physical hydrogeological property is sediment size influencing water flow (capillary action), water chemistry (weathering rates, geology), accessibility of sediments (interstitial space, colonisation) and migratory rates (stygobite fauna). The following sections describe and consider the results from this thesis in the context of the wider research areas. Implications and insights of the results and possible alternative explanations are considered.

Influence of the Devensian glaciation on stygobite fauna of fluviokarst and glaciokarst systems in the UK

High abundance and species richness was observed at sites in both the Peak District and Yorkshire Dales consistent with results from continental Europe (Dole-Olivier et al. 2009b), in particular the large numbers of copepods collected in the karst hyporheos (Deharveng et al. 2009, Galassi et al. 2009a, Galassi et al. 2009b). Interestingly, no large stygobite fauna (*Niphargus* sp. or *Crangonyx subterraneus*) were collected from either the Peak District or Yorkshire Dales, although records of *Niphargus aquilex* do exist as far north as Hartlepool, Teesside though records are sparse. While this survey was not exhaustive, the same sampling

methods collected numerous stygobite fauna from the chalk and sandstone hyporheic zones in the south of the UK. Where large stygobite crustaceans have been found further north, migratory pathways exist such as the river Severn and Thames allowing migration through alluvial gravels or migration through aquifers i.e Cretaceous chalk which runs as far north as Hartlepool. The hyporheic zone has been suggested as a major migratory pathway (Malard 2003) with the interstitial highway model proposed by Ward and Palmer (1994:148) describing alluvial aquifer systems as “evolutionary pathways and long-term dispersal routes for meiobenthic fauna”.

The possibility of further records of *Crangonyx* sp. and *Niphargus* sp. in the north of the UK cannot be ruled out, recently a stygobite *Crangonyx* sp. was discovered in Iceland which survived numerous glacial periods in sub-glacial refugia (Kristjansson and Svavarsson 2007). Small stygobite species are present in the Peak District and Yorkshire Dales, notably *Antrobathynella stammeri* which is present at both limestone sites (Stubbington et al. 2008), and one *Parastenocaris* sp. collected from the Yorkshire Dales with both species rare though notably north and south of the Devensian glacial limit. Increasing distance from the Devensian glacial limit does appear to affect the distribution of *Niphargus* sp. with distribution restricted to sites located in Southern and Central England. Research in continental Europe (Hof et al. 2008, Galassi et al. 2009b) and North America (Strayer et al. 1993, Varricchione et al. 2005, Lewis and Reid 2007) has found groundwater biodiversity to be affected by recent glacial events, species richness along river corridors increases as distance from the glacial limit also increases. Evidence also exists of the use of sub-glacial refugia in the UK (Stubbington et al. 2008), Europe (Lefebure et al. 2007), North America (Strayer et al. 1995) and Iceland (Kristjansson and Svavarsson 2007).

Spatial factors (latitude, longitude) are important drivers of stygobite biodiversity, richness and abundance in northern latitudes, particularly in relation to recent glaciations (Dole-Olivier et al. 2009b, Galassi et al. 2009a). Results from surface waters tend not to follow the

same pattern, with environmental factors more important than spatial factors in structuring species richness (Beche and Statzner 2009). There is an obvious time lag between surface and groundwater spatial distributions following glacial perturbations, with spatial and environmental factors affecting both communities to varying degrees though along different temporal gradients. The effects of the progression and regression of glaciations upon groundwater biodiversity occurs over long temporal periods in comparison to surfacewater biodiversity. Surface fauna have numerous dispersal mechanisms available with many adult species capable of flight, also passive dispersal mechanisms such as animal vectors and wind are commonly utilised by surface fauna. (Bilton et al. 2001)

During the progression of glacial events a wider range of refugia will exist for groundwater and hyporheic species in comparison to epigean species. Conversely colonisation during the regression of glacial events will be quicker for surface fauna with groundwater and hyporheic colonisation initially from sub-glacial refugia. It is known that due to the heat and high pressures at the base of moving glaciers meltwater occurs, this meltwater is forced down into the groundwater due to the immense pressure of the ice sheet (Lemieux et al. 2008). Glacial ice also contains a large amount of dissolved organic matter eroded during glacial progression (Hood et al. 2009). When the ice melts along the base of glaciers this will become available to taxa living in refugia beneath the icesheets. Increasing distance south of the southern limit of the Devensian glaciation clearly has an effect on species with limited dispersal mechanisms, with a clear north-south distribution of *Niphargus* species. Species able to survive glacial perturbations in groundwater refugia such as *A. stammeri* (Proudlove and Knight 2003) and *Crangonyx* sp.(Kristjansson and Svavarsson 2007) will be found in previously glaciated areas.

Trontelj (2009) suggests that macro-stygobiont ranges are rarely greater than 200km and found fourteen stygobiotic species with large ranges to be highly diversified, with the fourteen stygobiotic species splitting into a further 51 cryptic lineages. Distributions in the

UK of *Antrobathynella stammeri* and *Niphargus sp.* populations commonly exceed 200 km in distance, the possibility that previously described species could be morphologically similar and genetically different is a distinct possibility. Recent advances in the study of subterranean fauna, in particular the genetic basis of adaptation and convergent evolution within subterranean habitats can provide unique insights into the true biodiversity of subterranean habitats (Juan et al. 2010). Cryptic diversity and convergent evolution of many groundwater species can make the true spatial distribution of many of these taxa difficult (Lefebure et al. 2007). Convergent evolution has been a common theme in many groundwater and cave species, with Darwin (1859) describing cave species as “the wrecks of ancient life”. This description is partly true with recent molecular studies tracing back the isolation of calcrete populations in Western Australia to the Pliocene epoch (2-5 million years BP), a period when surface waters dried up and groundwaters remained possibly the only refugia (Byrne et al. 2008). A finding that adds weight to the theory of sub-glacial refugia in northern latitudes, where interglacial and glacial oscillations can also be measured in millions of years.

The influence of hydrogeology on groundwater-surfacewater connectivity

Hydraulic conductivity measurements taken from the chalk hyporheic indicated low hydraulic conductivity with vertical hydraulic gradients positive or neutral. It is likely that the strongly upwelling groundwater, fine sediments and associated low hydraulic conductivities combine to prevent surface water penetrating into the riverbed sediments to any great depth. The hyporheic zone in chalk catchments is possibly at a scale of a few centimetres, with the hyporheic zone in the classic sense not occurring in the alluvial sediments of the Frome and Piddle catchments. Similar results have been found in other chalk catchments (Pretty et al. 2006) and connectivity between chalk streams and the alluvium can be highly variable (Allen et al. 2010). The lack of significant groundwater and surface mixing in the chalk hyporheic sediments in this study may change at the catchment

scale when looking at losing and gaining areas along rivers. In two catchment scale studies on the Frome and Piddle catchments losing and gaining reaches were associated with specific geological strata, gaining reaches were associated with the Greensand/Chalk ($18\text{--}51\text{ L s}^{-1}\text{ km}^{-1}$) and Chalk/Palaeogene ($68\text{--}152\text{ L s}^{-1}\text{ km}^{-1}$) boundaries with substantial surface water losses occurring at the Broadstone Sand Formation ($158\text{--}171\text{ L s}^{-1}\text{ km}^{-1}$) (Arnott 2009). In the present study the results from the sandstone catchments were mixed with both catchments having high hydraulic conductivities. The proportions of fine sediments differed between the two sandstone catchments with the Tone having high levels of fine sediments whereas the Exe had a high proportion of coarse sediments in the hyporheic, with levels more similar to the two limestone catchments. The two sandstone catchments have high hydraulic conductivity readings with levels similar to those found in the two limestone catchments.

The influence of hydrogeology on physicochemistry of the hyporheic zone

Dissolved oxygen

Across all river catchments the general pattern was of lower dissolved oxygen availability at 50cm than 20cm depth. However, horizontal patterns were inconsistent suggesting that vertical patterns dominate in hyporheic sediments exhibiting both high and low hydraulic conductivity properties. The consumption of dissolved oxygen in the hyporheic zone is regulated by residence time of water flowing through the sediments and respiration rates driven by microbial activity (Baker et al. 2000). Fine sediments have a large surface area allowing microbial colonisation to increase resulting in increased oxygen uptake as water passes slowly through fine sediments. Coarse sediments have a smaller surface area and increased water flow resulting in oxygen reaching vertically deep into the hyporheic zone (Malard and Hervant 1999, Baker et al. 2000). Field and laboratory experiments have demonstrated that microbial activity in the hyporheic zone increases as hydraulic conductivity, oxygen availability and sediment surface area increase (Malard and Hervant

1999, Fischer et al. 2005, Navel et al. 2010) although human activity resulting in sediment clogging and channel modification can reduce lateral and vertical connectivity and inhibit microbial processes (Dahm et al. 1998).

The presence of fine sediment in the Frome and Piddle catchments had a mixed effect on oxygen levels at 50cm depth with levels in the Frome higher than records found across all other catchments. Dissolved oxygen levels at 20cm and 50cm depth across all river catchments were above levels shown to have a deleterious effect on salmonid egg survival (Malcolm et al. 2003) though cm^{-1} scale changes in oxygen at the surface would be undetected by the methods used in this study and a particular problem on chalk streams impacted from fine sediment input (Kemp et al. 2011). Studies have shown invertebrates cope better with decreasing dissolved oxygen levels than fish though when metabolic rates of invertebrates are high they will also suffer, active taxa will migrate vertically to areas of higher oxygen concentrations while less active taxa reduce their activity (Kolar and Rahel 1993). Individuals with low metabolic rates, for example early instar larvae or relatively inactive taxa perform better in low oxygen environments than later congeneric instar larvae (Davis 1975). The high abundance of copepods, in particular *Bryocamptus* sp. in the coarse limestone sediments suggests they have a greater oxygen requirement. In a similar study, Dole-Olivier et al. (2009b) also found *Bryocamptus* sp. to be strongly associated with limestone and high levels of dissolved oxygen.

Interestingly in this study the chalk catchments had relatively high dissolved oxygen levels in the hyporheic zone. In a recent study Nogaro et al. (2010) found the effects of fine sediments (clogging) to have highly variable effects on dissolved oxygen levels in the hyporheic zone with dissolved oxygen levels high ($9.5 \pm 0.3 \text{ mg/l}^{-1}$) in clogged sites at 50cm depth. Nogaro et al. (2010) suggest that irregular clogging still allows water to penetrate into the deeper sediment layers. Another possible explanation is that high subsurface flows in chalk karst are commonly associated with Palaeogene cover (MacDonald et al. 1998) with karstic flows in

the chalk possibly facilitating the penetration of oxygenated water to subsurface sediments, particularly in areas of the Frome and Piddle associated with the Palaeogene deposits.

Nutrients

Chalk sediments suffer from extensive clogging of the alluvial sediments a process which severely inhibit microbial activity in the deeper sediment layers (Brunke and Gonser 1997, Dahm et al. 1998). The catchments strongly associated with fine sediments (Frome, Piddle and Tone) were also the catchments with the highest levels of nitrates and the most agriculturally impacted. The role of denitrification in the hyporheic zone has been extensively studied, in particular in agriculturally impacted catchments similar to the Frome, Piddle and Tone (Hill 1996, Kaushal et al. 2008). The significant decrease in dissolved oxygen levels across all catchments except the Frome from the shallow to the deep hyporheic zone in this study was not paralleled by a decrease in nitrates, with dissolved oxygen at levels sufficient to limit denitrification processes within the catchments in this study. Denitrification has been shown to increase as levels of dissolved oxygen fall to $<2 \text{ mg/l}^{-1}$, and DOC levels are sufficient to support the process (Curie et al. 2009). The shallow hyporheic layer possibly occurring in chalk sediments was discussed in chapters 3 and 4. This shallow layer may induce a very short but steep chemical gradient, where levels of oxygen reduce to $<2 \text{ mg/l}^{-1}$ and the process of denitrification may occur, although in this study we detected no differences in nitrates at the scales used. In a study on the River Lambourne, a chalk stream in southern England, the hyporheic sediments were predominately aerobic and denitrification did not occur consistently (Pretty et al. 2006). Similarly, Rivett et al. (2007) found denitrification occurring in the saturated zones of Chalk, Sherwood Sandstone and Jurassic Limestone aquifers only once these aquifers became confined and dissolved oxygen was depleted.

Community respiration in aquatic systems is vitally important and thus has attracted considerable attention in both the benthic (Cummins 1974, Parker et al. 2005, Bott et al.

2006) and hyporheic zones (Malard and Hervant 1999, Storey and Dudley-Williams 2004). Energy fuelling communities in temperate lotic systems is derived from allochthonous organic matter from autumnal leaf litter (Kaushik and Hynes 1968, Reice 1974). All catchments had relatively high levels of organic material at 20cm and 50cm depth. Allochthonous material enters the hyporheic zone predominately during flood events, although fine and coarse particulate organic matter will penetrate into the hyporheic sediments at base flow if the interstitial space is sufficient. When turnover of sediment and organic matter occurs during flood events organic matter and sediment will be deposited as a heterogeneous mixture (Jones et al. 1995, Boulton and Foster 1998, Ward et al. 1998).

The influence of hydrogeology on species richness and abundance of the hyporheos

The hyporheos of the Frome, Piddle and Tone catchments had low species richness and abundance compared to the limestone sites. This difference in abundance and species richness can be explained by hydrogeology and associated properties (porosity, hydraulic conductivity) and thus interstitial pore space. As diversity and species richness increase abundance also increases as different communities become tightly packed within a given geographical area (MacArthur and Wilson 1967, Southwood et al. 1982). Morphological diversity also increases with species richness, as different species occupy multiple niches suitable for their specific morphology and ecological performance (Winemiller 1995). From the perspective of interstitial space the chalk hyporheos is a spatially homogeneous environment with few available spatial niches to exploit, conversely the limestone hyporheos is a spatially heterogeneous environment.

Niche differentiation occurs in the hyporheos with community composition and abundance highly variable temporally and spatially (Brunke and Gonser 1999). Brunke and Gonser (1999: 355) state that “epigean fauna occupy a fundamental niche whereas hypogean fauna occupy a realized niche”. Food web studies in cave systems have shown that rather than

relying on CPOM from terrestrial sources, stygobite consumers preferentially feed on epilithon and FPOM (Simon et al. 2003). In streams, epigeal and hypogean fauna have adapted to utilise available resources in their particular habitats. Many hypogean fauna exhibit low metabolic rates in response to scarce resources of DO and organic matter, whereas epigeal fauna have high metabolic rates in response to an increase in DO and organic matter (Hervant et al. 1996, Hervant et al. 1999). In this study *Gammarus* sp. and *Niphargus* sp. were often found at the same sites though at different depths with studies observing a close relationship between *Niphargus* sp. and *Gammarus* sp. (Fiser et al. 2007, Simcic and Brancelj 2007, Navel et al. 2011b). Organic matter processing by *Gammarus* sp. and production of FPOM can benefit *Niphargus* sp. which actively consumes FPOM (Navel et al. 2011b).

The seasonal use of the hyporheic zone by meiofaunal sized taxa varied between high and low groundwater levels. The seasonal dynamics of fauna in the hyporheic zone has been reported in numerous temperate stream studies, with temporal patterns occurring as various species develop through the seasons (Palmer 1990, Brunke and Gonser 1999, Olsen and Townsend 2003, Lencioni and Rossaro 2005). Vertical migration has also been linked with surface water flow as winter floods force taxa to move deeper into the hyporheic sediments when interstitial space is sufficient (Marchant 1995). The increase in meiofauna across all catchments during the winter and particularly in the limestone catchments will provide a prey resource for many juvenile and meiofaunal invertebrate predators (Swan and Palmer 2000, Schmid and Schmid-Araya 2002). The body size of macrofauna was proportionally greater across all catchments during summer with a sharp reduction in body size during the autumn, highlighting clearly the seasonal cycle from autumn hatching to summer emergence. This fluctuation between seasons makes the relatively stable body size of meiofauna between seasons increasingly important in providing a food resource for growing invertebrate predators and juvenile fish throughout the seasonal cycle. The Ure and Wharfe catchments

showed an increase in abundance of *Bryocamptus* sp. during the autumn at 50cm depth which could be a response to increased perturbations in the surface waters as rainfall levels are historically high during this period. The hyporheic zone can be a densely occupied habitat particularly when interstitial space becomes reduced (Strayer 1994). The controlled experiment showed habitat partitioning occurring amongst Chironomidae with body size increasing in the treatments containing coarse sediment. Similarly the role of macrofauna differed significantly with larger bodied taxa significantly reduced in the fine sediments indicating the role of meiofaunal sized taxa is of increasing importance in the fine sediment layers.

Salmonids have been shown to exhibit great plasticity in their diets reacting quickly to the available prey items, fish will reduce their selectivity as food availability becomes low and many fish species will be able to handle and consume *Gammarus* sp. (Reiriz et al. 1998). In response to fish predation *Gammarus* sp. have been shown to respond with increased avoidance behaviour by the use of refugia and reduced activity (Pennuto and Keppler 2008). The use of in stream refugia by *Gammarus* sp. has also been shown in chalk streams with utilisation of marginal macrophytes during the summer months allowing populations of *Gammarus* sp. to increase in the presence of their main predator the Bullhead (*Cottus gobio*) (Harrison et al. 2005). The presence of *Gammarus* sp. in the hyporheic zone could be a response to the large numbers of fish predators in the benthic zone, in particular the large numbers of bullheads commonly found in English chalk streams (Prenda et al. 1997, Harrison et al. 2005).

There is a strong link between salmonids, bullheads, *Gammarus* and detritus in chalk streams. In a study on Bere stream, a tributary of the River Piddle, a trophic cascade was detected where increased abundance of bullhead resulted in a reduction in detrital processing rates by *Gammarus* (Woodward et al. 2008). In the same study a strong negative density-dependence between bullhead and brown trout was also detected producing a “Trout-

Bullhead-*Gammarus*-Detritus” cascade (Woodward et al. 2008). The large numbers of *Gammarus* sp. in the chalk streams means the trophic link between *Gammarus* sp. and their predators is strong. Many of the ecological functions in the chalk streams are being performed by *Gammarus* sp. the dominant detritivores in the system. This also produces another trophic link into the deep hyporheic with *Niphargus* sp. potentially utilising the resultant FPOM from organic matter breakdown by *Gammarus* sp. (Navel et al. 2011b).

In comparison, the limestone catchments have a wide range of species albeit of a smaller size performing ecosystem processes within the limestone hyporheic. In coarse sediments the role of smaller meiofauna can increase hydraulic conductivity through the grazing of biofilms, for example Copepoda have been shown to reduce bacterial biomass by as much as 45% (Perlmutter and Meyer 1991). Increased hydraulic conductivity can further increase permeability as sediments are flushed during up and downwelling (Song et al. 2007). Grazing of biofilms containing high densities of microalgae by *Bryocamptus zschokkei* has been shown to significantly increase hatching success of ovigerous females (Brown et al. 2003), and subsequently boosting abundance and turnover. The coarse limestone sediments and accessibility of the interstitial pore spaces of the sediments allows oxygen and nutrients to be flushed deep into the hyporheic zone. Epilithic biofilms benefit from the available resources in the limestone hyporheic, and subsequently fauna feeding on the biofilms will also benefit which will in turn encourage biofilm growth and maintain hydrological connections between surface waters and the hyporheic zone.

Perlmutter and Meyer (1991) suggest that biofilms are a more important food source to microdetritivores than to macrodetritivores in streams, this uptake of biofilms helps to keep the interstitial pore spaces clear aiding hydraulic conductivity and providing a basal resource of energy within the system. Conversely, the lack of microdetritivores in the chalk hyporheic will increase the possibility of clogging and limit the prey of smaller taxa that would normally prey on small fauna during their early instar stages. This has left a niche which

seems to be filled by *Gammarus* sp. and *Niphargus* sp. which seem well adapted to proliferate in the chalk hyporheic sediments at the expense of a wider range of fauna.

Conclusion

Sediment composition strongly influences the physicochemistry, biology and hydrology in the hyporheic zone by controlling water flow through the sediment interstices (capillary action), which in turn influences the uptake and replenishment of available resources. Local geology and weathering rates directly influence sediment granulometry with large alluvial sediments characteristic of hard geologies, whereas fine alluvial sediments are characteristic of soft geologies. Local geology and associated alluvial sediments will influence the faunal assemblage living in the hyporheos, creating distinct “geological communities”. The results of this study clearly show the influence of granulometry on abundance and faunal assemblages associated with each “geological community”. In particular, faunal assemblages characteristic of coarse (limestone) and fine (chalk) alluvial sediments are quite distinct. Faunal assemblages associated with sandstone catchments contain biological and chemical characteristics of both the limestone and chalk communities. The large numbers of copepods found in the limestone sediments indicate that meiofaunal sized taxa penetrate deep into the hyporheic zone. High vertical connectivity between surface waters and the hyporheic in the limestone sediments provides replenishment of resources to the community living in the deeper sediment layers. Our results suggest that the copepod species *Bryocamptus echinatus* lives deeper in the hyporheic than other *Bryocamptus* species. Abundance of *Bryocamptus echinatus* did not differ significantly after a major flood event, whereas abundance of all other meiofauna reduced significantly. The utilisation of the deeper sediment layers by copepods occurred only on the coarse sediments in the limestone and the Exe catchments. Copepods often dominate the hyporheos in gravel bottomed streams (Hunt and Stanley 2003), having a preference for well sorted sediment layers in the hyporheic zone (Robertson and Milner 2006) and groundwaters (Galassi et al. 2009a). Chironomidae, Oligochaetae and

Nematoda become increasingly dominant in meiofaunal communities as substrate size decreases (Hunt and Stanley 2003). The low abundances of copepods in the fine sediments of the chalk and sandstone (Tone catchment) hyporheic zones reflects the decrease in sediment size in these catchments. The results from the experimental survey found copepods abundant across all sediment sizes which suggest the “tipping point” for Copepoda regarding sediment size was not reached.

The increased abundance of larger taxa in the hyporheic zones of the chalk and sandstone catchments seemed at first counter-intuitive, though on reflection the dominance of amphipods in the hyporheic zones of the fine sediments is not unusual. Records exist of the burrowing ability of stygobite amphipods, in particular in fine clay sediment layers (Culver et al. 2006). Also *Gammarus* sp. will migrate vertically into deeper sediment layers in response to perturbations such as floods (Stubington et al. 2010, Wood et al. 2010). The ability to burrow requires the displacement of sediment and in fine sediment layers this displacement is possible. Displacement of large, coarse sediments is difficult, with the ability to move in between the interstitial void spaces of greater importance. The smaller body size of *G. pulex* found in the limestone hyporheic in comparison to other catchments suggests that this is possibly the case, although other pressures will also influence the use of the hyporheic by fauna such as predation and competition. The hyporheic and associated “geological community” can be described quite distinctly with the chalk and limestone sediments diametrically opposite in granulometric properties and associated communities, “geological communities” inhabiting the gradient between chalk and limestone would contain a complex mixture of the chalk and limestone chemical and biological characteristics. The two sandstone catchments did contain elements of both the chalk and sandstone catchments with the two catchments quite distinct with the Exe catchments physico-chemical and biological properties closer to the limestone catchments with the Tone containing characteristics similar to those found in the chalk catchments.

Gerino et al. (2003) proposed a classification system based on mechanical activities rather than the consequences of those activities, in particular the role of bioturbation increasing in importance in the hyporheic zone as sediment size decreases. Regarding a functional role *G. pulex* are regarded as shredders, although they are omnivorous and will switch between predator and shredder depending on local resources (Kelly et al. 2002). The role played by *G. pulex* in UK chalk streams is particularly important, being the dominant fauna in many chalk systems, and capable of penetrating into the deeper sediment layers, performing key ecosystem functions in the process (bioturbation, shredding and predation). The use of the chalk hyporheic by a number of small instar Glossosomatidae, *Baetis sp.* and *Leuctra sp.* is possibly facilitated by the mechanical activity of *G. pulex* in the sediment layers. The North American amphipod, *Hyaella azteca*, which performs a similar role to *G. pulex*, will burrow rapidly in fine, organic-rich sediments in comparison to coarser sandy sediments, in the same study smaller *Hyaella azteca* also burrowed into the sediments in greater numbers than larger *Hyaella azteca* (Doig and Liber 2010).

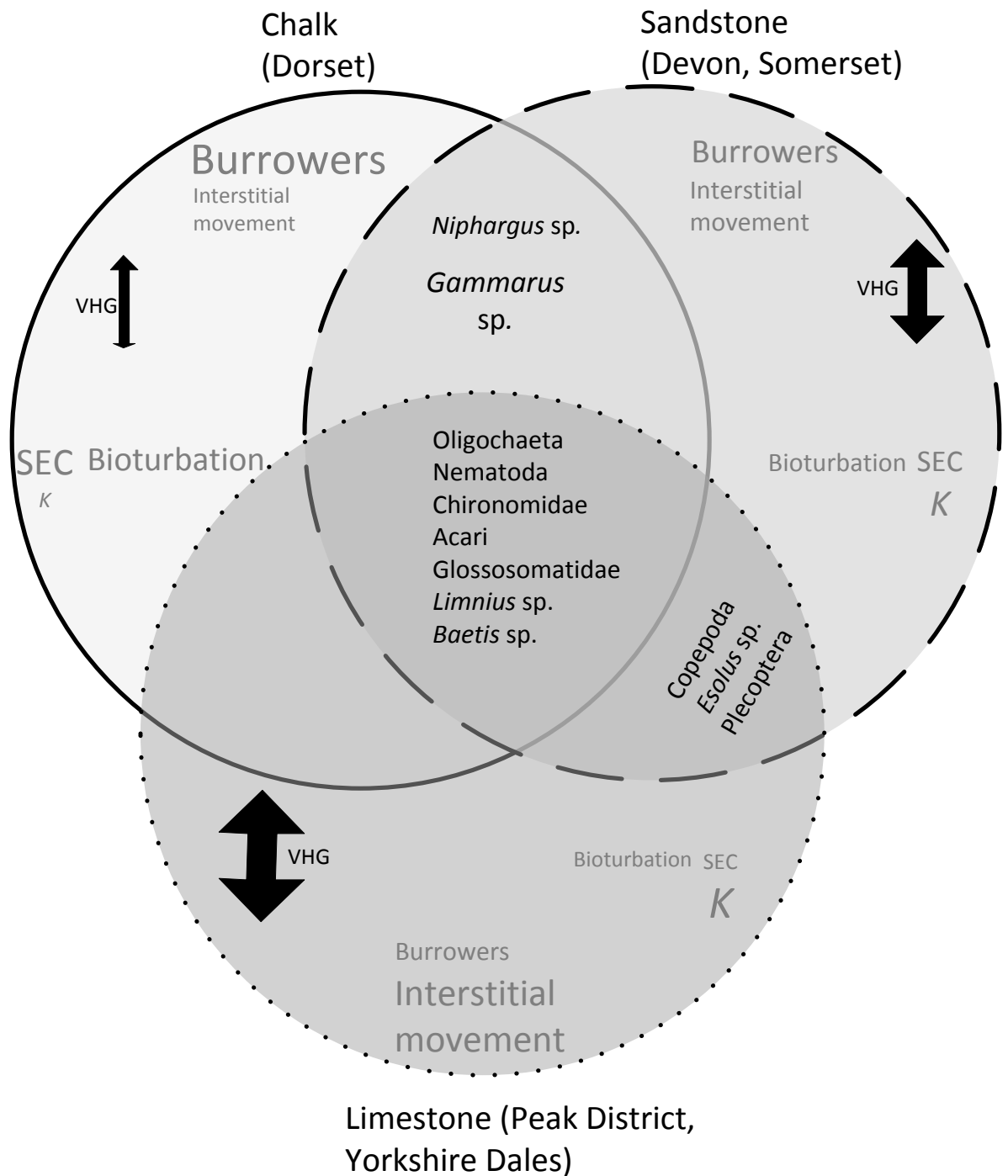


Figure 6.1. Abstract representation of main drivers influencing the hyporheos of Cretaceous Chalk – solid circle; Permo-Triassic Sandstone – dashed circle; Carboniferous Limestone – dotted circle. Black VHG arrows show strength of up- and downwelling observed in the hyporheic zone at each geological area. Width of black arrows indicates the strength of up- and downwelling with arrow point size indicating the relative strengths of upwelling (upward pointing arrow) and downwelling (downward pointing arrow). Grey text describes characteristic processes and physicochemical parameters observed at each geological area. Larger text size indicates a high importance of that physicochemical parameter with small text indicating a low importance of the respective physicochemical parameter. (VHG = vertical hydraulic gradient; SEC = specific electrical conductivity; *K* = hydraulic conductivity).

The use of *G. pulex* and Copepoda to describe processes in the hyporheic could be a useful tool, with the different mechanical properties of *Gammarus* sp. and copepods and their subsequent ability to utilise hyporheic sediments very different. Both *Gammarus* sp. and copepods are common across most aquatic systems and the impact of sedimentation on alluvial sediments is a problem in many rivers. The role of sediment size in shaping faunal assemblages in the hyporheic zone and the influence of sediment size on processes in the hyporheic zone is conceptualised in Figure 6:1. In fine sediments, mechanical processes, for example burrowing, performed predominately by *Gammarus* sp. will be important, with the resulting bioturbation from burrowing activities an important process in enhancing connectivity in fine sediment layers. Fine particulate organic matter derived from the shredding activities of *Gammarus* sp. may also feed down to deeper sediment layers with stygobite species, such as *Niphargus*, reliant on organic inputs from the surface. In coarse sediments, the need for bioturbation of sediments will be reduced, with connectivity between the surface and deeper sediment layers high. Inputs of coarse particulate organic matter will be able to penetrate into the deeper sediment layers with organic matter processing high, as replenishment of resources is in balance with demand. Burrowing through the sediment will be difficult with movement through the interstitial spaces increasing in importance. Species characteristic of coarse sediments will be small or elongated. The hyporheic zone is inherently patchy containing a range of sediment sizes and different sediment compositions at small spatial scales i.e. centimetres (patch types) metres (riffles). While variability within alluvial sediments will always occur the results from this study show that the influence of geology will be the primary determinant of sediment composition and hydraulic properties in the hyporheic zone.

The impact of glaciation on the stygobite fauna of the UK is still evident. The hyporheic faunal assemblages of the Yorkshire Dales and Peak District were very similar with only *Crangonyx subterraneus* found of the larger stygobite species collected from the Derwent

catchment, although abundance was very low. There were no records of *Niphargus* sp. in the two limestone sites with the distribution still restricted to sites in the south of the UK. The stygobite *Antrobathynella stammeri* was found in the Yorkshire Dales with abundance high. The appearance of *A. stammeri* in this study and other recent finds in the Peak District and in the south of the UK suggest that this species is rare though widespread and has possibly persisted in sub-glacial refugia during the last ice ages.

Area of future research

In the UK current climate predictions have forecast wetter winters and drier summers (Hulme 2002, Jackson et al. 2010) scenarios which will have a major impact on the ecology of rivers and streams. The use of the hyporheic by a range of fauna has been clearly shown in this study with sediment composition a strong driver of diversity across catchments. Similarly, the use of the hyporheic zone as a refuge from floods (Palmer et al. 1992, Olsen and Townsend 2005) and low flows (Wood et al. 2010, Datry 2011) has been shown in numerous studies. Accessibility of the hyporheic zone differs across geological areas with the ability of fauna to seek refuge from floods and dry periods also variable across geological river types. Further work on the use of the hyporheic zone as a refuge across a variety of hydrogeological conditions is required to assess the impacts on our rivers and streams from current climate scenarios, with potentially some streams i.e. limestone, potentially resilient to perturbations whereas chalk streams are potentially vulnerable to perturbations.

Recent studies have found methane derived carbon signals in stoneflies (Ayato et al. 2004, Reid 2007) and caddisflies (Trimmer et al. 2009). Reductive habitats requiring alternative energy or carbon sources are common in the hyporheic zone where dissolved oxygen concentrations can decrease rapidly. Methane is recognised as an important carbon and energy source in lake food webs (Jones and Grey 2011) and recently in river food webs (Trimmer et al. 2009) and floodplain aquifers (Reid 2007). The hyporheic zone could

contribute significantly to energy budgets in streams and rivers, particularly in highly productive hyporheic zones, i.e. limestone sediments. Understanding pathways of methane in groundwaters and the hyporheic zone and associated processes will help quantify energy budgets in streams and potential dampening of methane emissions to the atmosphere.

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Appendix

Appendix 1. Mean physicochemical values ($\pm 1SE$) from (a) summer survey (2008) at 20 and 50 cm, and (b) winter survey from 50cm depth. (DO=dissolved oxygen, cond = electrical conductivity, temp = temperature, PT = pump time, LOM = loosely associated organic matter)

Site	Value	pH	DO	cond	temp	Cl	NO ₃	SO ₄	K	Na	Ca	Mg	LOM	
Dorset														
Frome 20cm	Mean	7.80	7.22	542.33	18.05	15.05	13.54	2.96	1.43	9.63	42.67	2.08	0.08	
Dorset	SE	0.04	0.17	3.75	0.12	0.41	0.46	0.09	0.05	0.15	0.85	0.06	0.00	
Frome 50cm	Mean	7.78	6.55	545.46	17.58	15.95	11.76	3.43	1.63	9.95	52.76	1.61	0.13	
Dorset	SE	0.02	0.16	5.09	0.09	0.50	0.71	0.10	0.06	0.29	1.55	0.05	0.01	
Piddle 20cm	Mean	7.73	5.18	548.13	18.72	16.09	21.57	9.23	1.95	10.82	72.78	2.20	0.20	
Dorset	SE	0.05	0.18	13.51	0.30	0.39	0.99	0.21	0.06	0.29	2.09	0.05	0.01	
Piddle 50cm	Mean	7.55	4.27	532.67	18.49	17.42	22.24	10.46	2.05	12.09	90.06	2.12	0.15	
Devon	SE	0.06	0.23	15.02	0.25	0.30	1.06	0.45	0.10	0.21	2.15	0.04	0.02	
Exe 20cm	Mean	7.21	5.62	369.13	16.37	19.99	10.87	12.50	2.82	11.09	24.61	6.45	0.11	
Devon	SE	0.05	0.11	4.63	0.04	0.81	0.91	0.53	0.17	0.57	1.26	0.30	0.01	
Exe 50cm	Mean	6.88	2.71	336.04	16.10	20.93	8.35	12.83	2.77	12.53	28.43	7.47	0.25	
Devon	SE	0.04	0.12	7.59	0.04	0.91	1.00	0.48	0.17	1.09	2.26	0.45	0.03	
Tone 20cm	Mean	7.34	7.08	420.92	14.53	22.85	18.86	11.54	2.89	13.25	37.91	7.40	0.09	
Devon	SE	0.03	0.10	14.05	0.10	1.76	1.29	0.40	0.11	0.70	1.96	0.26	0.01	
Tone 50cm	Mean	7.10	5.50	490.58	14.38	20.62	22.79	12.73	3.15	12.16	59.10	5.96	0.16	
Yorkshire Dales	SE	0.04	0.15	19.50	0.10	0.86	2.09	0.48	0.14	0.35	2.61	0.28	0.02	
Ure 20cm	Mean	7.94	7.30	253.75	15.45	7.80	1.49	4.87	1.27	7.55	40.81	4.44	0.09	
Yorkshire Dales	SE	0.03	0.08	9.88	0.09	0.22	0.17	0.18	0.05	0.17	1.01	0.16	0.01	
Ure 50cm	Mean	7.68	4.37	270.54	15.28	8.80	1.17	5.90	1.35	7.81	41.14	4.47	0.12	
Yorkshire Dales	SE	0.03	0.16	9.38	0.10	0.21	0.11	0.23	0.04	0.14	1.13	0.16	0.01	
Wharfe 20cm	Mean	8.09	7.76	236.42	15.01	8.15	1.25	3.51	0.73	8.58	50.00	2.90	0.07	
Yorkshire Dales	SE	0.04	0.12	2.03	0.19	0.23	0.03	0.18	0.04	0.15	1.96	0.08	0.01	
Wharfe 50cm	Mean	7.81	5.12	259.88	14.61	9.37	1.29	3.55	1.08	9.34	51.46	3.04	0.20	
Peak District	SE	0.04	0.27	3.65	0.16	0.41	0.05	0.18	0.07	0.26	2.21	0.09	0.02	
Dove 20cm	Mean	7.71	8.66	446.67	13.48	14.76	6.70	13.17	2.84	16.47	57.46	7.70	0.15	
Peak District	SE	0.04	0.19	12.15	0.10	0.44	0.32	0.50	0.08	0.45	1.63	0.37	0.01	
Dove 50cm	Mean	7.59	7.45	462.96	13.46	14.77	6.98	15.84	2.99	15.31	67.90	8.56	0.17	
Peak District	SE	0.03	0.19	9.97	0.09	0.49	0.34	0.86	0.15	0.54	2.16	0.35	0.02	
Derwent 20cm	Mean	8.12	7.50	452.08	15.20	20.41	9.31	24.49	3.51	21.44	60.04	5.94	0.08	
Peak District	SE	0.04	0.20	7.11	0.27	0.68	0.42	1.00	0.11	0.45	1.45	0.18	0.01	
Derwent 50cm	Mean	7.93	5.27	467.54	14.91	18.94	6.70	22.53	3.69	20.00	67.70	4.86	0.16	
	SE	0.03	0.29	6.78	0.22	0.76	0.57	0.95	0.22	0.58	1.87	0.19	0.02	
(b)														
Dorset														
Frome	Mean	8.49	530.67	12.27	7.59	3.05	18.08	16.73	8.88	1.69	11.04	69.28	2.19	0.08
Dorset	SE	0.32	4.44	0.11	0.03	0.33	0.39	1.28	0.42	0.08	0.43	2.60	0.10	0.01
Piddle	Mean	7.22	590.79	12.44	7.39	2.75	15.62	11.89	7.26	2.18	11.97	88.72	2.35	0.15
Devon	SE	0.25	2.28	0.16	0.05	0.26	0.38	0.70	0.26	0.12	0.24	3.65	0.07	0.02
Exe	Mean	6.96	289.42	11.81	7.19	1.61	18.37	9.96	9.96	3.56	15.31	32.63	8.72	0.16
Devon	SE	0.18	6.32	0.13	0.06	0.21	1.05	1.76	0.39	0.20	0.92	2.37	0.52	0.02
Tone	Mean	7.63	354.33	11.86	7.34	1.53	15.37	13.59	6.85	2.62	10.40	36.45	5.20	0.11
Yorkshire Dales	SE	0.18	23.09	0.08	0.05	0.14	0.99	1.93	0.37	0.15	0.64	3.04	0.50	0.02
Ure	Mean	7.43	230.42	10.91	7.86	1.45	5.04	1.49	2.41	1.45	7.12	37.26	3.49	0.10
Yorkshire Dales	SE	0.23	17.44	0.09	0.03	0.13	0.23	0.14	0.14	0.09	0.25	1.69	0.18	0.01
Wharfe	Mean	8.05	257.54	10.35	7.76	1.54	6.78	1.48	1.53	1.26	7.23	37.67	1.81	0.15
Peak District	SE	0.26	5.55	0.10	0.04	0.16	0.19	0.03	0.08	0.05	0.24	1.15	0.13	0.02
Dove	Mean	7.38	392.33	9.71	7.60	1.35	16.73	9.14	19.39	1.82	9.49	68.12	6.76	0.22
Peak District	SE	0.51	11.90	0.16	0.04	0.13	0.83	0.54	1.42	0.18	0.37	2.46	0.37	0.02
Derwent	Mean	7.33	515.11	9.39	7.73	1.68	22.32	8.81	21.50	2.56	14.86	76.72	4.47	0.12
	SE	0.33	7.10	0.14	0.06	0.20	1.20	0.94	1.17	0.22	0.79	3.47	0.20	0.02

Appendix 2. Mean abundance of taxa collected per BOU-ROUCHE sample from 20 and 50cm depth from each river catchment. Samples were collected during June-July 2008. (Key a = adult; j = juvenile).

Site		Frome	Piddle	Exe	Tone	Ure	Wharfe	Dove	Derwent								
Taxa	Code	20cm	50cm	20cm	50cm	20cm	50cm	20cm	50cm	20cm	50cm	20cm	50cm	20cm	50cm		
<i>Bryocamptus zschokkei</i>	(Bz)	0.42	0.21	2.29	0.21	0.42	0.00	0.42	0.00	9.79	3.54	9.38	7.71	6.46	1.46	14.79	5.00
<i>B. minutus</i>	(Bm)	0.21	0.00	1.04	1.25	0.63	0.63	0.63	0.63	9.17	1.46	5.83	7.08	4.17	1.25	8.75	1.88
<i>B. echinatus</i>	(Be)	0.42	0.00	0.42	0.00	0.21	0.00	1.25	0.00	5.63	0.21	7.08	5.83	2.08	1.03	8.33	1.24
<i>B. pygmaeus</i>	(Bp)	0.00	0.00	0.00	0.83	0.00	0.00	0.00	0.00	1.46	0.83	0.00	0.00	3.33	2.08	7.92	1.46
<i>B. cuspidatus</i>	(Bc)	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>B. weberi</i>	(Bw)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.42	0.83	0.83	1.67	0.00	0.00	0.00	0.00
<i>Maraenobiotus</i> sp.	(Mar)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00
<i>Attheyella wulmeri</i>	(Aw)	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>A. bedens</i>	(Ab)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00
<i>A. crassa</i>	(Ac)	0.00	0.21	0.00	0.00	0.83	0.00	0.00	1.04	0.63	1.88	0.83	0.42	4.17	0.63	10.00	1.88
<i>A. trispinosa</i>	(At)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00
<i>Canthocamptus staphylinus</i>	(Cs)	0.21	0.00	0.00	0.00	0.83	1.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Moraria poppei</i>	(Mp)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.21	0.00	0.00	0.00	0.42	0.00
<i>Nitokra hibernica</i>	(Nh)	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>N. psammophila</i>	(Nps)	0.00	0.00	0.00	0.00	10.63	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Paracyclops</i> sp.	(Pa)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.67	0.83	1.88	4.58	0.63	0.00	0.00
<i>Acanthocyclops</i> sp.	(Aca)	0.00	0.00	0.00	0.00	0.83	0.00	0.21	0.00	1.88	0.00	0.83	2.29	1.88	2.71	2.50	2.29
<i>Diacyclops</i> sp.	(Di)	0.00	0.00	0.00	0.00	5.63	1.67	2.50	0.63	4.17	1.04	5.83	2.08	4.38	0.42	4.58	3.96
<i>Macrocyclops</i> sp.	(Ma)	0.00	0.00	0.00	0.00	0.42	0.21	0.00	0.00	0.00	0.00	0.00	0.00	3.75	2.71	0.00	0.00
<i>Euicyclops</i> sp.	(Eu)	0.00	0.00	0.00	0.00	0.00	0.00	1.04	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Chloroperla trispinosa</i>	(Ct)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.21	0.00	0.00	0.63	0.00	0.00	0.00
<i>Leuctra</i> sp.	(Le)	0.00	0.42	0.00	0.42	1.25	0.00	0.21	0.21	0.42	0.63	0.00	0.63	0.63	0.21	0.83	0.00
<i>L. inermis</i>	(Lei)	0.42	0.00	0.00	0.00	2.08	0.00	0.63	0.00	0.00	0.00	0.63	0.00	0.00	0.00	2.29	0.00
<i>L. hippopus</i>	(Leh)	0.42	0.00	0.00	0.00	0.21	0.00	0.00	0.00	2.92	1.67	2.50	0.83	3.13	1.04	1.46	0.00
<i>L. moselyi</i>	(Lem)	0.00	0.00	0.00	0.00	0.21	0.00	0.21	0.00	1.88	0.42	1.04	0.63	3.33	1.04	0.83	0.00
<i>L. geniculata</i>	(Lge)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.63	0.00	0.21	0.21
<i>L. fusca</i>	(Lef)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.29	0.00	0.00	0.00	0.21	0.00	0.83	0.00
<i>Nemoura</i> sp.	(Ne)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00
<i>Capnia</i> sp.	(Cap)	0.00	0.00	0.00	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.42	0.00
<i>Pterodidae</i> sp.	(Per)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.46	0.00	0.42	0.63	0.00	0.00	0.00	0.00
<i>Diura bicaudata</i>	(Dbi)	0.42	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.21	0.00	0.00	0.00
<i>Isoperla</i> sp.	(Iso)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.63	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ephemerella ignita</i>	(Eig)	0.63	0.00	0.21	0.42	1.25	0.42	0.00	0.00	0.63	0.42	0.42	0.00	1.25	0.21	1.67	0.21
<i>Centroptilum</i> sp.	(Cen)	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Baetis</i> sp.	(Bae)	0.42	0.00	0.83	0.42	6.67	1.46	0.63	0.21	0.21	1.04	1.67	0.42	0.00	0.21	7.92	0.83
<i>Caenis rivulorum</i>	(Cri)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.42	0.42	0.00	0.00	3.54	0.83
<i>Heptagenia</i> sp.	(Hep)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.83	0.21	1.25	0.42	0.21	0.00	0.00	0.00
<i>Ecdyonurus</i> sp.	(Ecd)	0.00	0.00	0.00	0.00	0.21	0.21	0.00	0.00	0.00	0.00	0.42	0.21	0.00	0.00	0.00	0.00
<i>Ephemera</i> sp.	(Eph)	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ephemera danica</i>	(Eda)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
<i>Athripsodes</i> sp.	(Ath)	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Timodes</i> sp.	(Ti)	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
<i>Polycentropus</i> sp.	(Pol)	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.21	0.00	0.00	0.00	0.00	0.00
<i>Glossosoma</i> sp.	(Gl)	1.46	0.21	0.83	0.21	0.42	0.21	0.63	0.00	1.25	1.04	6.04	0.83	3.13	0.42	2.50	1.25
<i>Agapetus</i> sp.	(Ag)	1.67	8.13	1.67	0.42	0.00	0.00	0.42	0.00	0.00	0.00	1.04	0.00	2.08	0.00	0.83	0.00
<i>Limnephilus</i> sp.	(Li)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00
<i>Sericostoma</i> sp.	(Ser)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
<i>Hydropsyche siltitai</i>	(His)	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00
<i>Rhyacophila dorsalis</i>	(Rd)	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
<i>Oulimnius</i> sp.	(Ou)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.08	0.00	0.21	0.00	0.00	0.00	0.21	0.00
<i>Elmis aena (j)</i>	(Eaj)	0.83	0.42	0.21	0.00	1.04	0.00	0.00	0.00	0.21	0.00	0.21	0.21	0.63	0.00	1.67	0.21
<i>E. aena (a)</i>	(Eaa)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.21	0.00
<i>Limnius volckmari (j)</i>	(lvj)	7.92	2.08	0.83	0.42	2.29	0.83	3.75	0.83	1.67	1.67	2.71	2.29	1.46	0.83	4.17	0.21
<i>L. volckmari (a)</i>	(Lva)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
<i>Esolus parollelepipidus</i>	(Epa)	0.00	0.00	0.00	0.00	0.83	0.21	0.21	0.00	5.21	0.42	0.83	0.00	0.00	0.00	0.00	0.00
<i>E. parollelepipidus (j)</i>	(Epi)	0.00	0.00	0.00	0.00	0.63	0.21	0.63	0.21	6.46	2.92	5.42	1.67	0.42	0.21	0.21	0.00
<i>Riolus cupreus</i>	(Rc)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Asellus aquaticus</i>	(Aa)	0.21	0.21	0.21	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	4.58	5.42	0.42	0.00
<i>Gammarus pulex</i>	(Gp)	8.75	1.46	7.08	1.46	1.88	0.63	3.96	0.63	0.00	0.00	0.00	0.00	1.67	0.42	6.67	1.88
<i>Antrobathynella stammeri</i>	(As)	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.42	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00
<i>Crangonyx subterraneus</i>	(Csu)	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Niphargus aquilex</i>	(Naq)	0.00	1.04	0.83	1.04	0.00	0.00	0.00	4.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>N. fontanus</i>	(Nfo)	1.25	0.83	0.00	1.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>N. kochianus</i>	(Nko)	0.00	0.00	0.00	1.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	(ch)	106.46	31.88	49.38	24.17	42.29	7.50	73.96	18.96	250.21	169.38	48.33	131.67	185.21	76.15	238.13	102.50
Oligochaeta	(ol)	23.54	9.38	17.71	7.08	18.54	4.17	32.29	9.58	26.46	9.38	20.00	25.00	75.83	32.44	82.08	24.17
<i>Dicranota</i> sp.	(di)	1.04	0.83	0.21	0.21	1.46	0.63	3.54	0.00	5.00	1.04	0.83	0.42	0.21	0.00	2.08	0.21
Acari	(ac)	1.67	0.00	1.46	0.21	2.92	5.83	7.08	1.46	10.83	4.79	12.08	17.29	6.88	2.54	8.13	2.92
Species richness	(Spri)	23.00	17.00	18.00	18.00	30.00	17.00	25.00	15.00	32.00	25.00	33.00	26.00	34.00	22.00	35.00	18.00

Appendix 3. Mean total abundance of taxa per BOU-ROUCHE sample collected at 50cm depth from each river catchment during October-November 2008.

Taxa	Code	Frome	Piddle	Exe	Tone	Ure	Wharfe	Dove	Derwent
<i>B. zschokkei</i>	(Bz)	0.00	0.00	0.00	0.00	9.17	10.83	0.83	0.42
<i>B. minutus</i>	(Bm)	0.21	0.21	0.00	0.00	3.33	11.46	0.21	0.00
<i>B. echinatus</i>	(Be)	0.00	0.00	0.00	0.00	13.54	18.54	5.21	5.63
<i>B. pygmaeus</i>	(Bp)	0.21	0.00	0.00	0.00	0.00	1.88	0.00	0.00
<i>B. cuspidatus</i>	(Bd)	0.00	0.00	0.00	0.00	0.00	6.46	0.63	0.00
<i>B. dacijs</i>	(Bd)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42
<i>B. typhlops</i>	(Bt)	0.00	0.00	0.00	0.00	0.00	1.04	0.00	0.00
<i>Schizopera</i> sp.	(Sch)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
<i>Maraenobiotus</i> sp.	(Mar)	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00
<i>A. wulmeri</i>	(Aw)	0.00	4.17	0.00	0.00	0.00	0.00	0.00	0.00
<i>A. bedens</i>	(Ab)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>A. crassa</i>	(Ac)	0.63	0.21	0.00	0.00	0.00	0.00	0.00	1.46
<i>A. wierzejskii</i>	(Awi)	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Elaphoidella</i> sp.	(El)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21
<i>M. poppei</i>	(Mp)	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00
<i>M. brevipes</i>	(Mb)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>N. hibernica</i>	(Nh)	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.00
<i>N. psammophila</i>	(Nps)	0.00	0.00	7.71	0.00	0.00	0.00	0.00	0.00
<i>Tachidius</i> sp.	(Ta)	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00
<i>Paracyclops</i> sp.	(Pa)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
<i>Acanthocyclops</i> sp.	(Aca)	0.00	0.00	0.83	0.42	3.54	13.96	0.63	4.38
<i>Diacyclops</i> sp.	(Di)	0.00	0.42	1.67	0.21	2.92	1.67	2.50	2.08
<i>Macrocyclus</i> sp.	(Ma)	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
<i>Chloroperla trispinosa</i>	(Ct)	0.00	0.00	0.21	0.00	1.04	2.08	0.00	0.42
<i>Leuctra</i> sp.	(Le)	0.00	0.00	0.21	0.00	0.00	0.00	0.63	0.00
<i>L. hippopus</i>	(Lh)	0.00	0.00	0.00	0.00	0.00	0.42	0.21	0.00
<i>Baetis</i> sp.	(Bae)	0.63	0.00	0.42	0.00	0.00	0.00	0.21	0.00
<i>Caenis rivulorum</i>	(Cri)	0.21	0.42	0.00	0.00	0.00	1.25	0.63	1.25
<i>Heptagenia</i> sp.	(Hep)	0.00	0.00	0.00	0.00	0.63	0.63	0.00	0.42
<i>Ephemera</i> sp.	(Eph)	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
<i>Tinodes</i> sp.	(Ti)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Polycentropus</i> sp.	(Pol)	0.00	0.00	0.21	0.00	0.00	0.21	0.00	0.00
<i>Glossosoma</i> sp.	(Gl)	0.63	0.63	0.00	0.21	0.21	0.00	2.29	0.21
<i>Agapetus</i> sp.	(Ag)	6.46	1.25	0.00	0.00	0.00	0.00	3.96	2.08
<i>Oecetis</i> sp.	(Oe)	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00
<i>E. aena</i> (j)	(Eaj)	0.21	0.00	0.00	0.00	0.00	0.21	0.21	0.00
<i>E. aena</i> (a)	(Eaa)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>L. volckmari</i> (j)	(Lvj)	0.21	0.21	0.21	0.21	0.83	1.04	0.21	0.00
<i>E. parallelepipedus</i> (a)	(Epa)	0.00	0.00	0.00	0.00	0.63	0.83	0.00	0.00
<i>E. parallelepipedus</i> (j)	(Ej)	0.00	0.00	0.21	0.00	2.08	3.33	0.42	0.00
<i>Gammarus pulex</i>	(Gp)	0.83	0.00	0.42	0.00	0.00	0.00	0.83	0.00
<i>Niphargus aquilex</i>	(Naq)	0.21	1.25	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	(ch)	31.46	11.46	10.63	30.83	277.29	91.46	107.71	60.63
Oligochaeta	(ol)	21.67	11.88	13.96	13.75	24.17	50.83	39.38	12.92
dicranota	(di)	0.00	0.42	0.00	0.42	0.21	0.00	0.42	0.42
Acari	(ac)	0.63	0.63	2.50	3.33	7.92	34.58	2.92	0.42
Species richness	(Spri)	16.00	14.00	15.00	8.00	16.00	20.00	22.00	16.00

Appendix 4. Mean abundance of taxa collected from the colonisation chamber treatments (total n = 80 replicates) from the two experimental trials from October and November 2009. Numbers given are mean abundance per treatment. Symbols (l = larvae, a = adult, e = early instar).

	October				November			
	Fine	Intermediate	Coarse	Control	Fine	Intermediate	Coarse	Control
<i>Bryocamptus. zchokkei</i>	43	47	37	52	22	8	14	15
<i>B. minutus</i>	5	19	16	12	3	3	4	7
<i>B. echinatus</i>	13	11	10	9	1	16	8	15
<i>B. pygmaeus</i>	0	1	0	2	0	0	0	1
<i>B. cuspidatus</i>	0	0	0	0	0	3	0	1
<i>B. weberi</i>	0	0	0	0	0	0	1	0
<i>Elaphoidella</i> sp.	0	0	0	0	0	0	1	0
<i>Canthocamptus</i>								
<i>staphylinus</i>	0	0	0	0	0	0	0	0
<i>Moraria poppei</i>	0	0	1	0	0	1	1	1
<i>M. brevipes</i>	0	0	0	0	0	1	0	0
<i>Paracamptus schmeili</i>	0	0	0	0	1	1	0	0
<i>Parastenocaris</i> sp.	0	0	0	0	0	0	0	0
<i>Paracyclops</i> sp.	0	0	2	1	1	2	3	3
<i>P. poppei</i>	0	0	0	0	0	0	0	0
<i>Cyclops</i> sp.	3	0	0	2	0	0	0	0
<i>Acanthocyclops</i> sp.	7	3	22	8	0	2	2	3
<i>Diacyclops</i> sp.	6	5	7	6	1	2	3	1
<i>Eucyclops</i> sp.	0	0	2	0	0	1	0	1
<i>Paracyclops</i> sp.	0	0	2	0	0	0	0	0
Dytiscidae	0	0	0	0	0	1	1	0
<i>Chloroperla</i>								
<i>tripunctata</i>	2	5	19	18	1	6	21	20
<i>Leuctra</i> sp.	1	4	3	1	1	1	0	1
<i>L. inermis</i>	0	0	1	0	1	0	0	0
<i>L. hippopus</i>	0	0	1	2	0	0	0	0
<i>L. moselyi</i>	0	2	0	0	0	1	1	3
<i>Ephemerella</i> sp.	0	0	0	0	0	0	0	1
<i>Baetis</i> sp.	0	1	0	5	0	1	1	3
<i>Caenis rivulorum</i>	0	0	1	1	0	1	0	1
<i>Heptagenia</i> sp.	0	0	0	0	0	1	0	1
<i>H. fusca</i>	0	0	0	0	1	0	1	0
<i>Plectonemia</i> sp.	0	0	0	0	0	0	0	0
<i>Polycentropus kingi</i>	0	1	0	1	1	0	0	1
<i>Glossosoma</i> sp.	0	0	0	0	0	0	1	1
<i>Limnephilus</i> sp.	0	1	1	2	1	0	1	3
<i>Ryacophila dorsalis</i>	0	0	0	0	0	0	1	1
<i>Oulimnius</i> sp.	0	0	0	3	0	0	1	1
<i>Elmis aena</i> (j)	0	0	0	0	1	0	0	1
<i>Limnius volckmari</i> (j)	0	0	0	0	1	0	0	3
<i>L. volckmari</i> (a)	0	0	0	1	0	0	0	0
<i>Esolus paralellopidus</i>								
(a)	0	2	4	13	1	6	9	14
<i>E. paralellopidus</i> (j)	1	2	3	0	2	2	0	3
<i>Gammarus pulex</i>	0	1	3	2	1	1	2	1
<i>Alona affinis</i>	7	7	18	13	4	1	1	1
<i>Chydorus ovalis</i>	0	0	0	0	0	1	0	0
Collembola (e)	1	0	0	0	2	2	1	1
<i>Hymenophorura nova</i>	0	1	1	1	0	1	1	1
<i>Anurida granaria</i>	2	2	2	3	0	0	1	1
<i>Folsomia</i> sp.	0	0	0	0	0	0	0	0
<i>Cryptopygus garreti</i>	0	0	0	0	1	1	1	1
<i>Deutaphorura inermis</i>	0	0	0	0	0	0	0	1
Collembola	3	3	3	4	3	4	4	5
Chironomidae	75	103	160	212	24	29	44	79
Oligochaeta	15	21	17	21	0	0	0	0
<i>Dicranota</i> sp.	2	1	2	1	0	0	0	1
Ostracoda	6	6	4	8	0	0	0	0
Acari	6	8	8	14	6	6	2	4