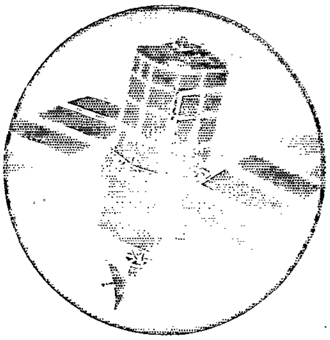
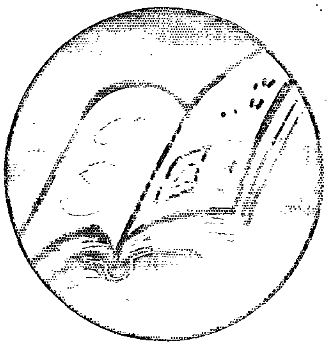
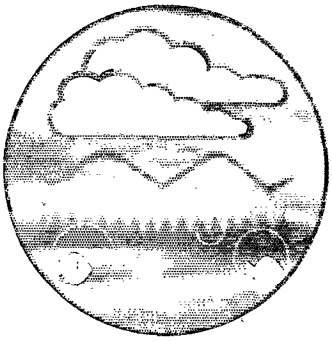
The Role of Bankside Habitat in River Ecology







Research and Development

Project Record
W1/F01/1

ENVIRONMENT AGENCY

The Role of Bankside Habitat in River Ecology

Project Record W1/F01/1

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Research Contractor:
Institute of Freshwater Ecology

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This R&D Project Record describes the ecology of aquatic invertebrates with respect to the bankside vegetation of chalk rivers and streams, and recommends guidelines for the management of riparian and marginal habitats.

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1.0 INTRODUCTION

River management, whether it be dredging, weed control, channel straightening or water abstraction, will have varying effects on river organisms and these are likely to be most marked on the bankside habitat (instream marginal zone). A number of recently completed or ongoing projects funded by English Nature and the Environment Agency (Mainstone *et al.*, 1998; Raven *et al.*, 1998; Ward *et al.*, 1998) have addressed problems associated with low flows, invertebrate association with habitat types, and various aspects of river corridor management and river habitat surveys. However none of these studies have addressed in a holistic sense the marginal zone of rivers.

The interactions between plants, their effects on flow hydraulics and the associated fauna of invertebrates, fish, birds and mammals, are most highly developed in the bankside habitat. In certain rivers this may provide most of the faunal diversity and furnish cover for both adult and juvenile fish. This area requires basic research to support, underpin and enable development of optimal management procedures. Knowledge of this habitat is essential in order to sustain faunal and floral diversity, encourage the continuance of 'natural' habitats, and follow the succession and evolution of bankside development.

The work reported here focuses on chalk streams which represent perhaps the most important European river habitat type in terms of conservation, and which are under increasing pressure as a result of water abstraction and agricultural practices. Chalk streams have been identified as a key habitat by the UK Biodiversity Steering Group (1995); and are the only UK river systems for which Biodiversity/Habitat Action Plans are being developed.

The work integrates with NERC Science Budget Project T11064G2 (Modelling faunal and floral response to reduced flows and habitat loss in a river. An experimental approach) which has made some preliminary investigations of bankside habitat and examined the seasonal resilience/constancy of faunal communities of mesohabitats in chalk streams. In addition the study has investigated the role of instream macrophyte growth on habitat availability. Furthermore the project fits well with the objectives set out for the NERC/NRA (now Environment Agency) scoping study on Catchment Ecosystem R&D including the underpinning of management decisions with basic science and the multidisciplinary and holistic approach which are of particular importance in anthropogenically disturbed lowland rivers. In addition the project provides a link with ongoing Environment Agency projects such as the River Habitat Survey by providing data at a finer scale which can be used to formulate best practice guidelines for achieving cost-effective functional management while maintaining ecological value.

The three broad objectives of the project are:

1) To describe quantitatively and qualitatively the fauna and flora of bankside and permanent instream marginal habitats of rivers.
2) To examine and analyse the functional dynamics of this habitat in response to natural seasonal effects and different management regimes.
3) To develop best practice guidelines to optimise management procedures with respect to both functional and ecological aspects.

2.0 SUMMARY

This study represents two and a half years of practical research and analysis of riparian vegetation and aquatic invertebrate interactions.

The prime objective of the first year was to determine the distribution and abundance of invertebrates in three different types of chalk stream habitat:

- bankside (stream margin)
- main channel gravel
- main channel *Ranunculus*

Ten streams were chosen, to enable comparisons to be made across a large number of differing physical and biological factors. These ten steams are described in Table 2.1 (see also Map, pg. 5). During initial field observations, it was apparent that there were several distinct types of riparian management which directly affected the quality and quantity of bankside and instream habitat, and therefore potentially influenced invertebrates in the stream.

These management types were:

- ungrazed (fenced, abundant tall vegetation) (Plate 2.1, page 7)
- grazed by cattle (short-grass banks only) (Plate 2.2, page 7)
- woodland (continuous tree-canopy cover) (Plate 2.3, page 7)

The ten streams all fell within the River Frome and River Piddle catchment areas in South Dorset, and following further inspection several types of bankside vegetation were distinguished, and sampled. These included:

- reeds and other monocotyledonous plants
- overhanging vegetation (*Urtica dioica*, *Rubus fruticosus* etc.)
- grass, at the edge of grazed margins
- *Apium* and *Rorippa*

In addition to sampling the various instream and marginal habitats across the different management regimes, the terrestrial (emergent) adults of aquatic invertebrates were also collected to determine whether they associated with particular riparian vegetation types, which were:

- the accessible aerial parts of trees
- tall herbaceous plants (such as *Symphytum officinale*, *Oenanthe crocata* and *Epilobium* spp.)
- short riparian grass
- the aerial parts of reeds

Table 2.1. Location, physical dimensions and occurrence of stretches of different bankside management regime of each stream. (W – woodland, G – grazed, U – ungrazed).

Stream	Map Ref. (NGR)	Mean depth (m)	Mean width (m)	Stretches		
				W	G	U
Frome side-channel (Lewell)	SY 739902	0.60	8.7		✓	✓
Piddle (Lower)	SY 850922	0.46	8.8		✓	✓
Piddle (Middle)	SY 805937	0.36	5.8	✓	✓	✓
Tadnoll brook	SY 794870	0.42	4.6	✓		✓
Cerne river	SY 666000	0.34	4.6		✓	✓
Bere stream	SY 852936	0.30	6.2	✓	✓	✓
Hooke river^1	SY 558985	0.26	2.8		✓	✓
Wynford Brook^2	SY 585965	0.16	2.0	✓	✓	✓
Devil's Brook^3	SY 779995	0.36	2.1		✓	✓
Milbourne stream^3	SY 813955	0.16	1.25		✓	✓

Superscripts denote streams which were subsequently discarded from the programme for the following reasons: ^{1} Suspected organic pollution, ^{2} Excessive siltation, ^{3} Dried up.

Table 2.2. The orientation (reading upstream → downstream, left to right) of individual stretch types, at each stream site.

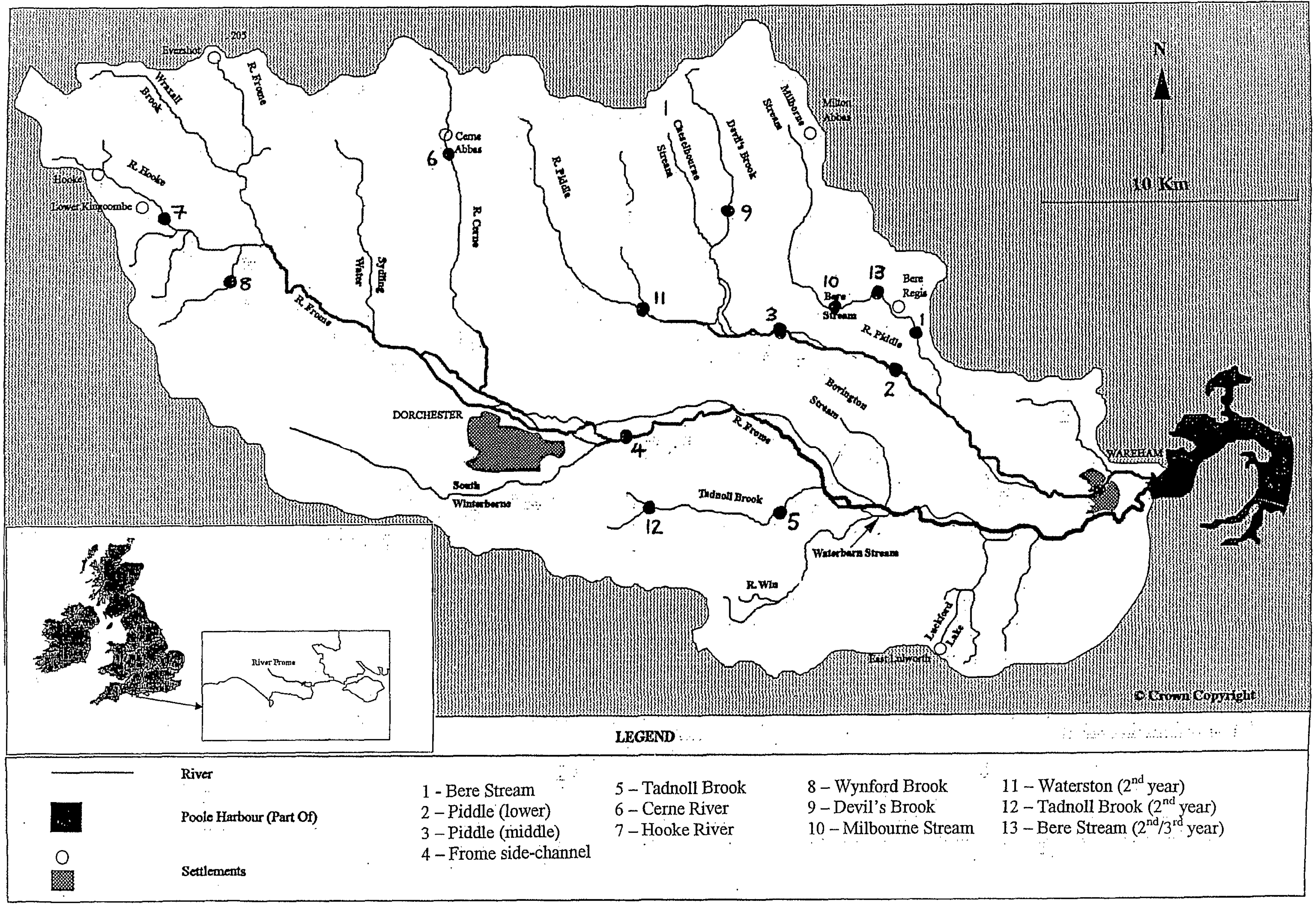
Stream	Orientation of stretch-types
Frome side-channel (Lewell)	Ungrazed --- Grazed
Piddle (Lower)	Grazed --- Ungrazed
Piddle (Middle)	Woodland --- Ungrazed --- Grazed
Tadnoll brook	Woodland --- Ungrazed
Cerne river	Ungrazed --- Grazed
Bere stream	Ungrazed --- Grazed --- Woodland
Hooke river^1	Ungrazed --- Grazed
Wynford Brook^2	Woodland --- Grazed --- Ungrazed
Devil's Brook^3	Ungrazed --- Grazed
Milbourne stream^3	Ungrazed --- Grazed

Three questions were asked of data that were gathered in the first year:

- **Was there any significant difference between the abundance and community composition of aquatic invertebrates in stream reaches that differed with respect to the types and extent of terrestrial riparian vegetation?**

There was little difference in overall invertebrate community between habitats from the three different reach types – woodland, grazed and ungrazed. Individual families, however, did show important differences between reaches, particularly in ungrazed compared to grazed reaches. Factors that may be responsible for these differences include greater oviposition by adults, which were more abundant in areas of well-developed bankside vegetation and the greater suitability of well-vegetated, undisturbed banks for beetle pupation. The shallow, silty 'pondlets' typical of grazed margins favoured some groups, including bugs and molluscs. Areas of abundant terrestrial

FROME & PIDDLE CATCHMENT



LEGEND

River

Poole Harbour (Part Of)

Settlements

1 - Bere Stream
2 – Piddle (lower)
3 – Piddle (middle)
4 – Frome side-channel
5 – Tadnoll Brook
6 – Cerne River
7 – Hooke River
8 – Wynford Brook
9 – Devil's Brook
10 – Milbourne Stream
11 – Waterston (2nd year)
12 – Tadnoll Brook (2nd year)
13 – Bere Stream (2nd/3rd year)

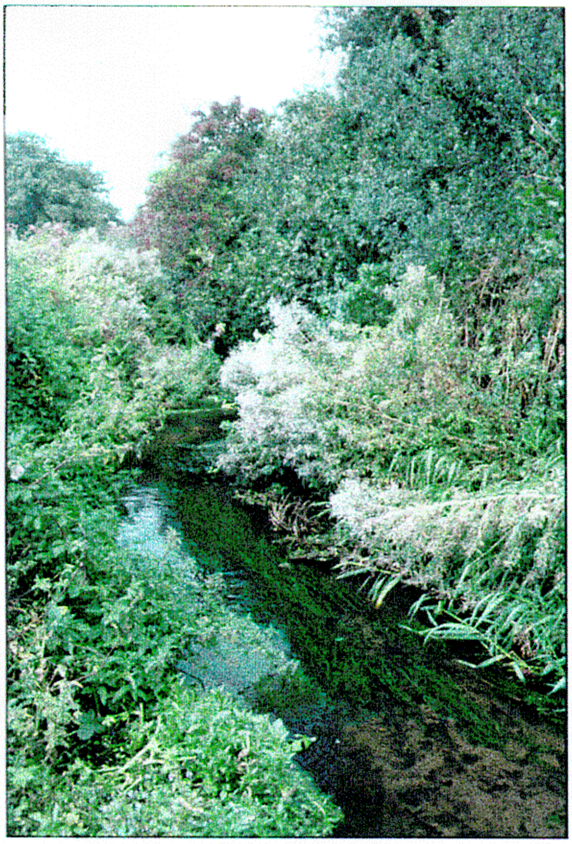


Plate 2.1: 'Ungrazed'
(Tadnoll Brook, September 1996)

Plate 2.2: 'Grazed'
(Hooke River, July 1996)

Plate 2.3: 'Woodland'
(Bere Stream, September 1996)

Plate 2.4: Diverse vegetation typical of ‘ungrazed’ regimes

Plate 2.5: A fenced stretch, on the lower Piddle

Plate 2.6: Vegetation typical of ‘grazed’ sections

Plate 2.7: A grazed stretch, also on the lower Piddle

bankside vegetation, including woodlands, may act as sources of aquatic insect recruitment, via greater adult oviposition in these areas. They may also be more favourable for beetle pupation. Abundance and diversity of aquatic invertebrates is thus likely to be greater in reaches with abundant bankside vegetation. These functions of bankside vegetation are likely to operate across a wide range of streams and rivers.

- **Was there any difference between the individual species abundance and community composition of aquatic invertebrates in the three habitats (main channel gravel, *Ranunculus* and vegetated margins) investigated?**

There were strong differences between the three habitats sampled: mid-channel gravel, *Ranunculus* and vegetated margins. Although gravel communities were always distinct, *Ranunculus* communities on occasions shared some similarities with those of margins. There were characteristic suites of invertebrates that were strongly associated with each habitat. Margins had a particularly large group. In the margins, there were particularly high numbers of snails, bugs, large beetles, fly larvae, small fish and damselfly nymphs. Many factors may have explained this faunal distribution, including differences in physical structure and complexity, food resources, flow and predation pressure across habitats. Many taxa may have been temporarily in the margins because of recent oviposition in the habitat by terrestrial adults. More invertebrate adults and egg masses were found in the marginal zone, consistent with it playing an important role in insect reproduction in streams, both as a conduit through which adults could leave and enter the water in relatively benign conditions and as a site for oviposition.

The greatest invertebrate abundance per sample was found in *Ranunculus*, due to the large numbers of baetid mayflies and *Simulium* blackfly larvae found in this habitat. Numerically, therefore, *Ranunculus* was the most important habitat. However, the margins appeared more important for the invertebrate assemblage as a whole. The invertebrate assemblage in the margins was both more diverse than mid-channel gravel and *Ranunculus* and showed greater equitability than the other habitats. Marginal vegetation was also relatively more important for invertebrates than the other habitats, based on measures of relative abundance per taxon. Mid-channel gravel and *Ranunculus* thus appeared to be more 'specialist' habitats, numerically dominated by relatively few species and unfavourable for many species. Margins were more 'generalist', less numerically dominated by few taxa and favourable for all but a few taxa. At the same time, there was a larger number of taxa that were only found in margins, compared to ones only found in gravel or *Ranunculus*.

- **Was there any difference between the abundance and community composition of aquatic invertebrates in different types of marginal vegetation?**

There was little difference in invertebrate community composition between different types of marginal vegetation, indicating that all margins were functionally broadly similar. There were minor differences between margins for particular groups of invertebrate, including bugs and small fish. This was due to two factors – differences between individual margins (for example, the presence of shallow, warm 'pondlets' in grazed margins) and differences between margins across different reaches (due to adults being more attracted to different types of terrestrial vegetation and ovipositing in those areas).

The stems and leaves of overhanging terrestrial vegetation trailing in the water appeared to be as favourable a habitat as semi-emergent aquatic marginal vegetation, such as watercress. The abundance of this important habitat in streams may be less dependent on aquatic factors, such as flow conditions, sediment characteristics and nutrient content of water than on the nature of bank management. Although different marginal types appeared to have similar invertebrate assemblages, they may have different functions with respect to oviposition. Tall emergent vegetation, including overhanging vegetation, may attract more terrestrial adults than floating grasses or semi-emergent macrophytes, such as watercress. More research is needed in this area. The extent of margins appeared to be relatively unimportant for several invertebrate groups, particularly caddis, beetles and damselflies, for which the nature of the terrestrial bankside vegetation may be the dominant factor in their abundance and distribution.

The second and third years consisted of experiments which were designed around the results of the first-year survey. Three sites were used:

The abandoned FBA site at Waterston near Puddletown	(NGR: SY 744953)
Tadnoll brook at Warmwell cress-farm	(NGR: SY 746875)
The upper reach of the Bere stream at Roke cress-farm	(NGR: SY 837958)

A variety of experiments were undertaken at these sites:

- **Investigation of the role of vegetated margins in 'buffering' the interactions between fish (*Cottus gobio,* the bullhead) and stream invertebrates.**

One of the important functions of margins in streams may be to provide refugia for invertebrates from fish. *Gammarus pulex* and the bullhead *Cottus gobio* are dominant species in chalk streams. Investigation into interactions between these two species has shown that bullhead can strongly influence the distribution and abundance of *Gammarus*. Experiments with artificial exclosures and substrata showed that the presence of fish was the dominant factor in the distribution of *Gammarus* in the two streams investigated. In the absence of fish, *Gammarus* showed little preference for either vegetation or gravel as a microhabitat. In natural habitats in summer, *Gammarus* was very much more abundant in margins and rare in gravel, particularly large individuals. Fish showed the opposite distribution, being common in gravel and rare in the margins, suggesting a strong negative correlation in the distribution of the two species. In winter, bullhead were found to be abundant in margins and somewhat less so in gravel. *Gammarus* showed the opposite distribution, being abundant in gravel and rarer in margins. This demonstrated a habitat shift by the two species, the distribution of bullhead possibly driving that of *Gammarus*. The spatial separation of the two strongly interacting species in summer, with *Gammarus* using the margins as a predation 'refuge', is likely to contribute to population stability for both species. This feature of margins buffering fish-invertebrate interactions may also have important implications for other species and contribute to high diversity and abundance of invertebrates in chalk streams, particularly for groups vulnerable to fish predation, such as large-bodied beetles, bugs and molluscs.

- **Examination of the specific role of bankside trees on the ecology of stream invertebrates, via their effect on terrestrial adult distribution and abundance (with specific reference to the glossosomatid caddis *Agapetus fuscipes*).**

This investigation demonstrated that the presence of trees was a strong influence in the distribution of terrestrial adults. They were caught in greater numbers near to trees, rather than far away, suggesting that they associated with trees for at least part of their lives. Early instar larvae and eggs were found in greater abundance either under or near to trees, consistent with adults ovipositing in these areas. Drift, dispersal and mortality may have all contributed to the distribution of later instars, which showed little correlation with proximity to trees along the reaches investigated. Bankside trees thus appeared to indirectly influence the distribution of larval *Agapetus* through their influence on terrestrial adults. Trees, and other terrestrial bankside vegetation, may exert an important influence on the distribution of many other species of aquatic insect though their effect on terrestrial adults; the value of woodland in maintaining insect diversity is well known. It is also highly likely that the interface between a block of woodland and an open stretch may be as important an area for adult insects as the trees themselves. Overall, streams with poorly developed bankside vegetation may have a reduced population of some insect species because of the lack of adult habitat.

- **Examination of the influence of riparian vegetation on the distribution of adult and aquatic insects.**

Sweep samples, sticky traps, drift traps and benthic samples were all taken in order to correlate insect distribution with particular types of riparian vegetation. This preliminary investigation showed that different vegetation types and different times of day affected adult insect distribution. Sweep samples taken over two 24-hour periods showed a strong diel movement of many dipteran and trichopteran families between areas of woodland and open areas. The nature of the movement varied from taxon to taxon, and the abundance of insects caught generally increased in the evenings both in woodland and open areas. Sticky traps only showed a significant longer-term difference in the distribution of Baetidae, Sialidae and Simuliidae between woodland and open areas, with the distribution of many other insects comparable between the two regimes. Long-term similarities thus appear to mask short-term movements. Factors affecting the insects, and upon which the riparian vegetation has an effect, may include the site of larval emergence, oviposition requirements, predation pressures, and abiotic components such as air temperature, air humidity and wind speed. It is likely that both large and small insects may for example use woodland areas as a refuge from both desiccation and predation during the day, but may choose to oviposit in more open areas when conditions allow. It is thus highly likely that most adult insects make use of more than one vegetation type both on a day-to-day basis and in the long-term.

The conclusions drawn from these experiments have clear implications for the management of riparian areas. These are discussed in Section 9.0, where the findings of the project are used to suggest the most beneficial policies for management of bankside areas, in terms of the requirements of aquatic invertebrates.

3. THE IMPACT OF RIPARIAN MANAGEMENT ON AQUATIC INVERTEBRATES.

3.1 Introduction

During the past century, much of the natural riparian vegetation along streams and rivers in the UK has been modified by agricultural practices and flood defence schemes. Riparian vegetation can have major impacts on stream organisms and ecosystem functioning, including the input of organic material (Cummins *et al.*, 1989; Whiles & Wallace, 1997; Pozo *et al.*, 1997), light and temperature regimes (Behmer & Hawkins, 1986; Sweeney, 1993), water chemistry (Ormerod *et al.*, 1993) and substrate composition (Maridet *et al.*, 1996; Wohl & Carline, 1996). Most studies investigating the effects of riparian vegetation on stream invertebrate communities have largely focused on the aquatic larval stages and their responses to the physical changes to the aquatic habitat. Far fewer studies have looked at the impact of riparian vegetation management on the terrestrial adult life-stages, although it has long been known that there are intimate links between the two (Macan, 1961; Macan & Worthington, 1968). Riparian vegetation is being increasingly recognised as an important factor in the ecology of adults (Jackson & Resh, 1989; Sweeney, 1993; Collier & Smith, 1998; Harrison & Hildrew, 1998). Recent research on the ecology of adult aquatic insects has also demonstrated their importance in the distribution and abundance of aquatic larvae, over small scales within lotic and lentic systems (Enders & Wagner, 1996; Bunn & Hughes, 1997; Harrison & Hildrew, 1998). Potentially, therefore, any changes to the riparian landscape could have important consequences for invertebrate abundance and diversity in streams, via its effect on terrestrial adults.

The natural state of most lowland chalk streams in the UK is an ill-defined, braided channel running through alder (*Alnus glutinosa*) and willow (*Salix* spp.) woodland (Ladle & Westlake, 1995). Since before Roman times, chalk catchments have been gradually cleared of the natural woodland, such that little remains. Almost all riparian trees and woodlands within catchments have also been cleared, or prevented from re-generating by over-grazing. Streams now flow mostly through arable and pasture fields, many of which are abandoned water-meadows. In contrast to the large physical influences of riparian vegetation on stream morphology, hydrology and temperature in run-off streams, groundwater-fed chalk streams have a much greater independence from terrestrial conditions, particularly temperature and water supply (Berrie, 1992; Ladle & Westlake, 1995). The substrate of flinty gravel is determined largely by the relatively high gradient of most chalk streams, rather than by local riparian influences (Ladle & Westlake, 1995). The abundance of in-stream macrophytes also lessens the relative importance of allochthonous input from riparian trees (Dawson, 1976; Vought *et al.*, 1998).

Marginal vegetation is abundant in spring-fed chalk streams, due to extremely stable flows and low stream power. Banks experience little erosion and are typically shallow. Riparian vegetation characteristics in any location are thus determined largely by local agricultural practices, rather than by interactions between fluvial hydraulics and local topography/geology. In the headwaters, the low bank profile allows ready access for cattle and sheep to almost all parts of the stream. Grazing animals can therefore have very strong impacts on riparian vegetation along chalk streams, both due to trampling of the water's edge when they drink from the stream and the high palatability of emergent vegetation. Where fences prevent cattle from reaching the stream banks, riparian and marginal vegetation grows luxuriantly. If kept from the stream for long enough, small blocks of woodland can develop. Typically a single stream will have several distinct types of bankside vegetation along its length, ranging from grazed sections, with little bankside vegetation, to woodland sections. This property of chalk streams makes them suitable sites to study the local effects of bankside vegetation on macroinvertebrate communities, especially the distribution of terrestrial adults. The stable flow regimes and similarity of aquatic habitat across different vegetation types also makes it easier to assess the influence of terrestrial adult distribution and behaviour on larval distribution and abundance. In many run-off streams, periodic flood events will extensively re-distribute larvae, such that they are dispersed many metres away from oviposition sites.

This investigation was conducted on chalk stream tributaries of the Rivers Frome and Piddle in Dorset, UK. Concern is growing over the effect of cattle grazing along the banks of these streams, particularly in the effect this can have on brown trout (*Salmo trutta*) populations, via the removal of the extensive marginal vegetation and overhanging cover (Giles & Summers, 1996). Fencing streams from stock is now being canvassed as a means of restoring the conservation and fishing potential of chalk streams (Giles & Summers, 1996). Little is known of the effects this may have on invertebrate communities. The objectives of this study were to investigate the influence of different agricultural management regimes along the streams on macroinvertebrate communities, both of aquatic and terrestrial life-stages.

3.2 Methods

3.2.1 Streams

Ten chalk streams, tributaries of the rivers Frome and Piddle, Dorset, UK, were selected for study, following initial field observations in April 1996. These streams were selected on the basis of a) overall physical similarity and b) the occurrence along each stream of stretches characterised by different bankside vegetation growth, due to changes in management regime. These stretches were either a) 'Woodland' (W), b) 'Grazed' (G), c) 'Ungrazed' (U). The length of stretches was approximately 50-100m, and while some stretches were immediately adjacent to other stretches, none was more than 200m from the next, along individual streams. The investigation was performed using ten different streams (rather than, say, ten wooded stretches on the same stream) in order to avoid pseudo-replication. The location and size of these streams is provided in Table 2.1, and the orientation of individual stretch types within these streams is shown in Table 2.2, both on page 4.

3.2.2 Management regime characteristics

a) Terrestrial characteristics

Woodland. Stretches were fenced from grazing stock. Riparian trees were present for at least 10m away from each bank and formed a closed canopy over the stream. Trees were predominantly Alder (*Alnus glutinosa*) and Willow (*Salix* spp.). The dominant wet marginal habitat was the stems and leaves of some of these terrestrial plants, largely ivy (*Hedera helix* L.), bramble (*Rubus fruticosus* L.) and Water-dropwort (*Oenanthe crocata* L.), which were overhanging the bank and trailing in the water. The sparse ground vegetation under trees along the bank was largely:

Nettle (*Urtica dioica*),
Bramble (*Rubus fruticosus*),
Ivy (*Hedera helix*),
Water-dropwort (*Oenanthe crocata*),
Elder (*Sambucus nigra*),
Other young trees.

Ungrazed. Stretches were fenced from grazing stock (for at least three years, prior to sampling). There were occasional riparian trees, although these were generally only on one bank and there was little shading of the stream by tree canopies. The abundant tall vegetation along the bank was dominated by:

Semi-aquatic grasses (*Glyceria maxima (Hartm.)* Holmb. and *Catabrosa aquatica* L.),
Sedges (*Carex* spp.),
Rushes (*Juncus* spp.),
Comfrey (*Symphytum officinale*),
Meadowsweet (*Filipendula ulmaria*),
Bittersweet (*Solanum dulcamara*),
Bramble (*Rubus fruticosus*),
Thistles (*Cirsium* spp.).
Hogweed (*Heracleum sphondylium*),
Water-dropwort (*Oenanthe crocata*),
Black Nightshade (*Solanum nigrum*),
Willowherb (*Epilobium* spp.),
Elder (*Sambucus nigra*),
Nettles (*Urtica dioica*),

As the year progressed, it became impossible to distinguish between separate patches of marginal vegetation, as increasing growths of trailing terrestrial vegetation 'coalesced' with emergent macrophytes. Marginal vegetation encroached greatly into the channel during the summer, such that in some areas it completely enclosed the channel.

Grazed: Stretches were fully accessible to grazing stock (sheep or cattle) on both sides. Bankside vegetation was characterised by a closely grazed short sward of grass, right up to the water's edge, and *Apium*, both of which were grazed by cattle. The structure of the margins was different, compared with ungrazed stretches. Cattle grazing and drinking at the water's edge caused the banks to slope more gradually into the water, creating a series of silty, marginal berms and 'pondlets'. Grazing by cattle prevented the grasses and *Apium* from growing into the main channel to any great extent.

b) Aquatic characteristics

Each stream was characterised by a bed substrate of coarse gravel (2-5cm diameter), abundant growths of Water-crowfoot (*Ranunculus* spp.) and abundant marginal emergent vegetation (for a fuller description of chalk streams, see Ladle & Westlake, 1995). Stretches were selected that had similar substratum characteristics, slope and flow conditions. Bank height in all stretches was between 20-30 cm above the water surface. Stretches differed chiefly in the extent of *Ranunculus* and marginal vegetation.

Woodland. Due to the low light conditions under canopy shade, there was only sparse *Ranunculus* and marginal vegetation. Small patches of *Ranunculus* were present, in areas of the stream under canopy gaps, together with occasional clumps of marginal Fool's Water-cress (*Apium nodiflorum*), Reedmace (*Typha latifolia*) and Bur-reed (*Sparganium erectum*). The dominant marginal habitat was the stems and leaves of terrestrial vegetation, largely ivy, bramble and Water-dropwort, which were overhanging the bank and trailing in the water.

Ungrazed. These stretches had abundant *Ranunculus* and marginal vegetation. The dominant marginal macrophyte was Fool's Watercress. There was extensive marginal growth of the semi-aquatic grasses *Glyceria* sp. and *Catabrosa aquatica*. Clumps of Reedmace and Bur-reed were also common. The trailing stems and leaves of rushes, grasses, Water-dropwort, Comfrey, Willowherb and thistles also formed an abundant aquatic habitat. As the year progressed, it became impossible to distinguish between separate patches of marginal vegetation, as increasing growths of trailing, terrestrial vegetation 'coalesced' with emergent macrophytes. Marginal vegetation encroached greatly into the channel during the summer, such that in some areas, it completely enclosed the channel.

Grazed. As for ungrazed stretches, there was abundant *Ranunculus* and marginal vegetation. However, the grasses *Glyceria* sp. and *Catabrosa aquatica* were as common as *Apium nodiflorum*, which was grazed by cattle. The structure of the margins was somewhat different, compared to ungrazed stretches. Cattle grazing and drinking at the water's edge caused the banks to slope more gradually into the water and creating a series of silty, marginal berms and 'pondlets'. Grazing by cattle prevented the marginal vegetation from growing into the main channel to any great extent.

3.2.3 Sampling regime

Two separate invertebrate sampling regimes were carried out. The first sampled aquatic habitats and the second the terrestrial bankside habitat.

Aquatic habitat

Invertebrates were sampled from up to three habitats in each stretch, if present. These habitats were a) Mid-channel gravel b) *Ranunculus* patches c) Marginal vegetation. Samples were taken using a standard 15-second kick- or sweep-sample with a 0.9mm-mesh long-handled pond net, a technique commonly used in other studies (Jenkins *et al.*, 1984; Ormerod, 1987; Rutt *et al.*, 1989; Wright, 1992, Pardo & Armitage, 1997). The gravel substrate was kick-sampled (where the substrate is 'kicked' with the foot just upstream of the net, so that dislodged invertebrates are swept into the net by the current) and the two other vegetated habitats were sweep-sampled (where the net is 'poked' into the vegetation, working upstream). The invertebrates caught in the pond net were transferred to a polythene bag and immediately preserved in 70% alcohol. Samples were sorted in the laboratory within three to five months, and the invertebrates counted and identified to the highest possible taxonomic level.

Each stretch of each stream had abundant coarse gravel (one of the criteria for site selection). Three patches of gravel were sampled in each stretch. Patches were selected that had both similar flow regimes and substrate size. Patches of above- or below-average flow (such as may be encountered where the current was channelled between patches of *Ranunculus*, or downstream of a *Ranunculus* bed) were avoided.

Three patches of *Ranunculus* were sampled in a similar manner. Again, patches were selected that were visually similar. No *Ranunculus* was sampled in woodland habitats, due to its rarity.

Samples of marginal vegetation were taken for each type of margin present in the stretch. For Grazed stretches in May, this included patches of floating, marginal grass and patches of *Apium*. For Woodland stretches, only the sparse trailing terrestrial vegetation was sampled, patches of emergent aquatic vegetation being too rare. In Ungrazed stretches, several types occurred, including *Apium*, *Typha*, *Sparganium* and trailing terrestrial vegetation. As for gravel and *Ranunculus*, three patches of each type of marginal habitat were sampled per stretch. No attempt was made to avoid sampling the mineral substrate underneath marginal vegetation.

Terrestrial habitat

The terrestrial adult stages of aquatic insects were sampled in each stretch, from mid-morning to mid-afternoon, using a standard sweep net. Vegetation was swept for 30 seconds. Insects and vegetation caught in the net were transferred to a plastic bag and immediately preserved in 70% alcohol. Several types of vegetation were sampled from each stretch, depending on its nature. In grazed stretches, the only dominant vegetation was short grass. In woodland stretches, two types of vegetation were sampled - the lower branches, twigs and leaves of trees and the sparse tall herbs underneath the trees. In ungrazed stretches, the lower branches of any trees present, the terrestrial portion of marginal vegetation and terrestrial tall herbs were all sampled. Adult insects were sorted in the laboratory and identified to family level.

3.2.4 Sites and Timing

Samples were taken at the same sites in May, July, September 1996 and January 1997. Two streams were discarded from the sampling programme from July onwards, because they dried up (Milbourne stream and Devil's Brook). One further site (Wynford stream) was discarded from the analysis because of excessive siltation of stretches under study. A fourth stream was discarded due to organic pollution (Hooke River). In July, September and January, it was increasingly difficult to distinguish between distinct patches of marginal vegetation in the ungrazed stretches, as the vegetation types increased in density and merged with trailing terrestrial vegetation. Accordingly, samples were taken of a single category ('marginal vegetation') in September and January.

3.2.5 Data Analysis.

The three samples taken from each habitat type in stream stretches (gravel, *Ranunculus*, margin) were combined to give a mean sample score for that habitat. This was done to reduce the small-scale variation in habitats within a stretch, such as that due to minor changes including flow and substratum characteristics.

Differences in invertebrate communities between stretches were addressed in two ways. Firstly, a multivariate approach was used, where the whole community in each habitat type from the different stretches was analysed, using ordination and classification techniques. This assessed whether there was any overall community difference between habitats in each stretch (e.g. mid-channel gravel habitat in woodland, ungrazed and grazed stretches). Secondly, a univariate approach was used, where the abundances of individual taxa (in this analysis, taxa were analysed at the family level) were compared for each habitat between different stretches.

Ordination and classification

Ordination was conducted on the samples from different stretches and seasons, for each habitat, using log-transformed ($\log_{10}$ x +1) family abundance data. A Principal Components Analysis was used, using the statistical package CANOCO (Ter Braak, 1987), following analysis of the lengths of ordination axes (all < 3 s.d.). Sample scores from the first axis of the ordination were compared across management type (grazed, ungrazed and woodland) and season, for each habitat type, using 1-way ANOVAs. Samples of log-transformed family abundance data from each habitat were also classified, using the TWINSPAN statistical package (Hill, 1979). The TWINSPAN hierarchy was followed to end-groups that could not be further subdivided.

Analysis of abundance of individual families

Due to the variation in taxon abundance between different streams, which may have masked differences between stretches, a comparison was made between stretches for taxa from the same stream. This was done by calculating the mean difference in abundance for each family between different stretches on each stream. In this approach, each stream had to possess both types of stretch under comparison (a minimum of three streams, for statistical analysis). It was thus possible to compare ungrazed and grazed stretches (five streams possessing both types of stretch) and ungrazed and woodland stretches (three streams possessing both types of stretch). It was not possible to compare grazed and woodland stretches, as only two streams (Bere stream and Middle Piddle) possessed both types of stretch. Thus, in this analysis, ungrazed stretches are compared to grazed stretches and ungrazed are compared to woodland stretches.

For example, the mean difference for *Calopteryx splendens* between margins in Ungrazed and Grazed stretches is the mean of the five differences calculated by subtracting the 'grazed' value from 'ungrazed' value for each of the five streams having both stretches. If there is no mean difference, this value should be 0. The statistical significance of the mean values obtained in this manner were calculated by performing a single value t-test on the five data points, with the null hypothesis that there is no difference (i.e. hypothetical mean = 0).

$$t\ \text{obs} = \frac{(X_{\text{ungrazed}} - X_{\text{grazed}}) - \text{null hypothetical mean}}{\text{Standard error of five data points}}$$

The difference between family abundance in ungrazed vs grazed stretches was thus calculated for each family for each of the three habitats: gravel, *Ranunculus* and margin.

3.3 Results

3.3.1 a) List of species/taxa encountered during survey across six streams 1996-1997

CADDIS
Adicella sp.
Agapetus fuscipes
Anabolia nervosa
Athripsodes albifrons
Athripsodes cinereus
Athripsodes sp.
Beraeodes minutus
Brachycentrus subnubilus
Ceraclea sp.
Drusus annulatus
Goera pilosa
Halesus radiatus
Hydatophylax infumatus
Hydropsyche pellucidula
Hydropsyche siltalai
Hydropsyche sp.
Hydroptila sp.
Ithytrichia sp.
Lasiocephala basalis
Lepidostoma hirtum
Limnephilus lunatus
Limnephilus politus
Lype reducta
Molanna angustata
Mystacides azurea
Oecetis sp.
Odontocerum albicorne
Oxyethira sp.
Polycentropus flavomaculatus
Polycentropus irroratus
Polycentropus sp.
Potamophylax cingulatus/latipennis
Rhyacophila dorsalis
Sericostoma personatum
Silo nigricornis
Ylodes sp.
Leptoceridae indet.

SNAILS
Ancylus fluviatilis
Acroloxus lacustris
Bithynia tentaculata
Lymnaea palustris
Lymnaea peregra
Lymnaea stagnalis
Physa fontinalis
Planorbis planorbis
Planorbis vortex
Planorbis other
Potamopyrgus jenkinsi
Sphaerium sp./*Pisidium* sp.
Succinia sp.
Theodoxus fluviatilis
Valvata cristata
Valvata piscinalis

BEETLES
Agabus bipustulatus
Agabus didymus
Agabus paludosus
Agabus sp.
Anacaena sp.
Brychius elevatus
Dryops sp.
Dytiscidae sp.
Elodes sp.
Elmis aenea
Gyrinus urinator
Haliplus fluviatilis
Haliplus lineatocollis
Haliplus obliquus
Haliplus sp.
Helophorus brevipalpis
Helophorus grandis
Helophorus other
Hydrobius fuscipes
Hydroporus discretus
Hydroporus tesselatus
Ilybius fuliginosus
Laccobius bipunctatus
Laccophilus hyalinus
Laccophilus minutus
Limnius volckmari
Ochthebius sp.
Orectochilus villosus
Oreodytes sanmarkii
Oulimnius tuberculatus
Platambus maculatus
Potamonectes depressus

MAYFLIES
Baetis spp.
Brachycercus harrisella
Caenis luctuosa
Caenis rivulorum
Centroptilum sp.
Ecdyonurus dispar
Ephemera danica
Ephemerella ignita
Heptagenia sulphurea
Paraleptophlebia sp.

DIPTERA
Ceratopogonidae
Chironomidae
Curculionidae
Dicranota sp.
Dixa sp.
Empididae
Limnephila sp.
Limnophora sp.
Psychodidae
Ptychopteridae
Rhagionix sp.
Simulium sp.
Stratiomyiidae
Tabanus sp.
Tanypodinae
Tipula sp.

AMPHIPODA
Gammarus pulex
Asellus aquaticus
Crangonyx pseudogracilis
Ostracoda

TRUE BUGS
Corixidae sp.
Gerris lacustris
Hesperocorixa sahlbergi
Hydrometra stagnorum
Micronecta poweri
Nepa cinerea
Notonecta glauca
Plea leachi
Sigara dorsalis
Sigara venusta
Velia caprai
Other Corixidae

ODONATA
Calopteryx splendens
Calopteryx virgo
Coenagrion puella
Cordulegaster boltonii

STONEFLIES
Leuctra fusca
Leuctra geniculata
Leuctra nigra
Isoperla grammatica
Nemurella picteti

LEECHES
Erpobdella octoculata
Glossiphonia complanata
Helobdella stagnalis
Theromyzon tessulatum
Piscicola geometra

FISH
Cottus gobio
Phoxinus phoxinus
Gasterosteus aculeatus
Lampetra planeri

MISCELLANEOUS
Sialis fuliginosa
Hydracarina
Oligochaeta
Lumbricidae
Tricladida
Austropotamobius pallipes

3.3.1 b) List of families/orders encountered during survey of six streams 1996-1997

Trichoptera
Leptoceridae
Limnephilidae
Hydroptilidae
Hydropsychidae
Polycentropodidae
Goeridae
Brachycentridae
Glossosomatidae
Lepidostomatidae
Odontoceridae
Rhyacophilidae
Sericostomatidae
Psychomyiidae
Beraeidae
Molannidae

Coleoptera
Dytiscidae
Elmidae
Hydrophilidae
Gyrinidae
Haliplidae
Helodidae
Hydraenidae

Hemiptera
Corixidae
Gerridae
Hydrometridae
Nepidae
Notonectidae
Pleidae
Veliidae

Mollusca
Ancylidae
Bithyniidae
Lymnaeidae
Sphaeriidae
Planorbidae
Hydrobiidae
Succineidae
Neritidae
Valvatidae
Physidae

Diptera
Athericidae
Ceratopogonidae
Chironomidae (excl. Tanypodinae)
Tanypodinae
Circulionidae
Culicidae
Tipulidae
Dixidae
Empididae
Muscidae
Psychodidae
Ptychopteridae
Rhagionidae
Sciomyzidae
Simuliidae
Stratiomyidae
Tabanidae

Crustacea
Gammaridae
Asellidae
Ostracoda
Astacidae

Ephemeroptera
Baetidae
Caenidae
Heptageniidae
Ephemeridae
Ephemerellidae
Leptophlebiidae

Odonata
Calopterygidae
Coenagriidae
Cordulegasteridae

Plecoptera
Leuctridae
Perlodidae
Nemouridae

Hirudinea
Erpobdellidae
Glossiphoniidae
Piscicolidae

Other
Sialidae
Hydracarina
Oligochaeta
Tricladida

Fish
Cottidae
Cyprinidae
Gasterosteidae
Petromyzonida

3.3.2. Physical differences between stream stretches of different management type ('woodland', 'ungrazed' and 'grazed' stretches)

For each stream, the difference between measurements from stretches of each management type was calculated. A one-sample t-test was then performed on these differences (log-transformed), with a null hypothesis of no difference between management types. Mean physical differences (log-transformed) between stretches of different management type are shown in Fig. 3.1, with significant differences indicated. The top panels show mean differences in depth, overall width and width of vegetated margin between ungrazed and grazed stretches; the lower panels show differences between ungrazed and woodland stretches. It was not possible to compare woodland with grazed stretches because only two streams analysed had both management types along their courses, which was insufficient for statistical analysis.

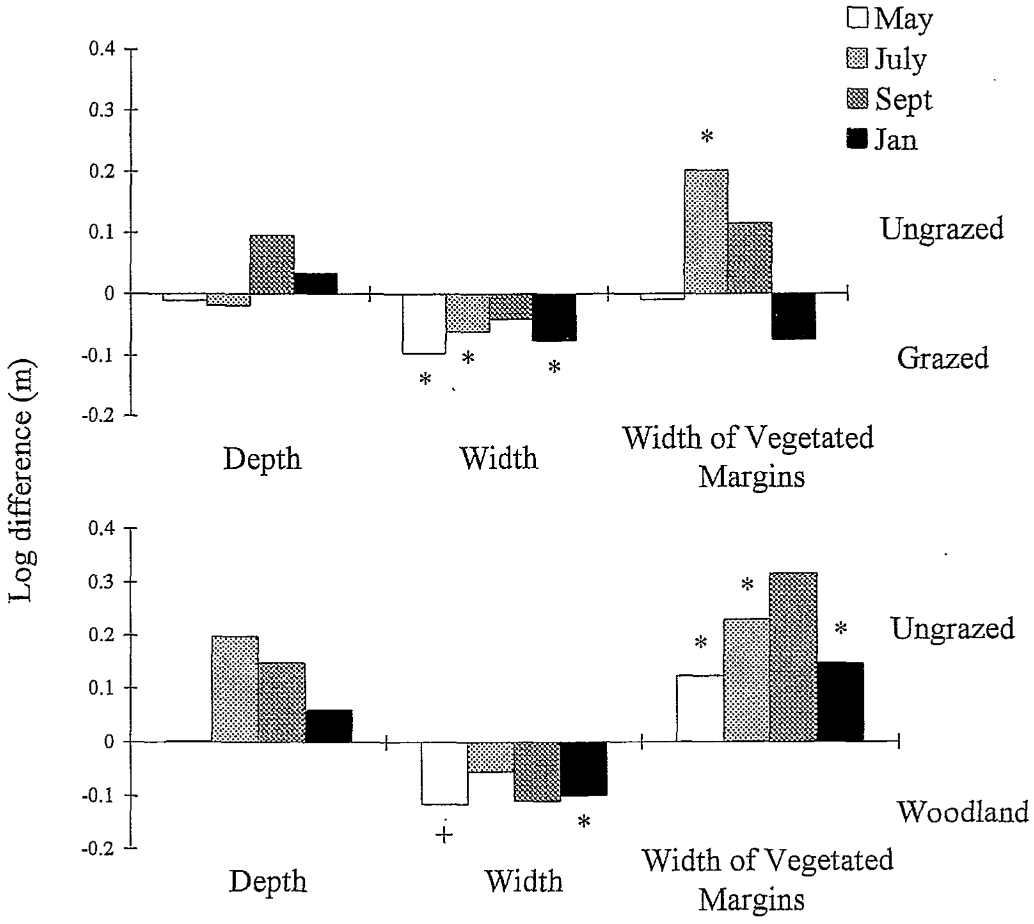


Figure 3.1
a, top panel) Mean difference in log-transformed Depth, Width and Width of Vegetated Margins between 'Grazed' and 'Ungrazed' stretches.
b, bottom panel) Mean difference in log-transformed Depth, Width and Width of Vegetated Margins between 'Ungrazed' and 'Woodland' stretches.

There was little overall difference in depth between grazed and ungrazed stretches (Fig. 3.1, top panel). Grazed stretches were significantly wider, from bank to bank, in May, July and January than ungrazed stretches. The width of vegetated margin was also significantly greater in ungrazed reaches in July. Although ungrazed stretches were deeper than woodland for most of the year, the difference was not significant (Fig. 3.1, lower panel). Woodland stretches were significantly wider than ungrazed stretches in May and January. Width of vegetated margin was significantly greater in ungrazed reaches in May, July and January.

3.3.3 Ordination of invertebrate communities in each habitat across different management and season

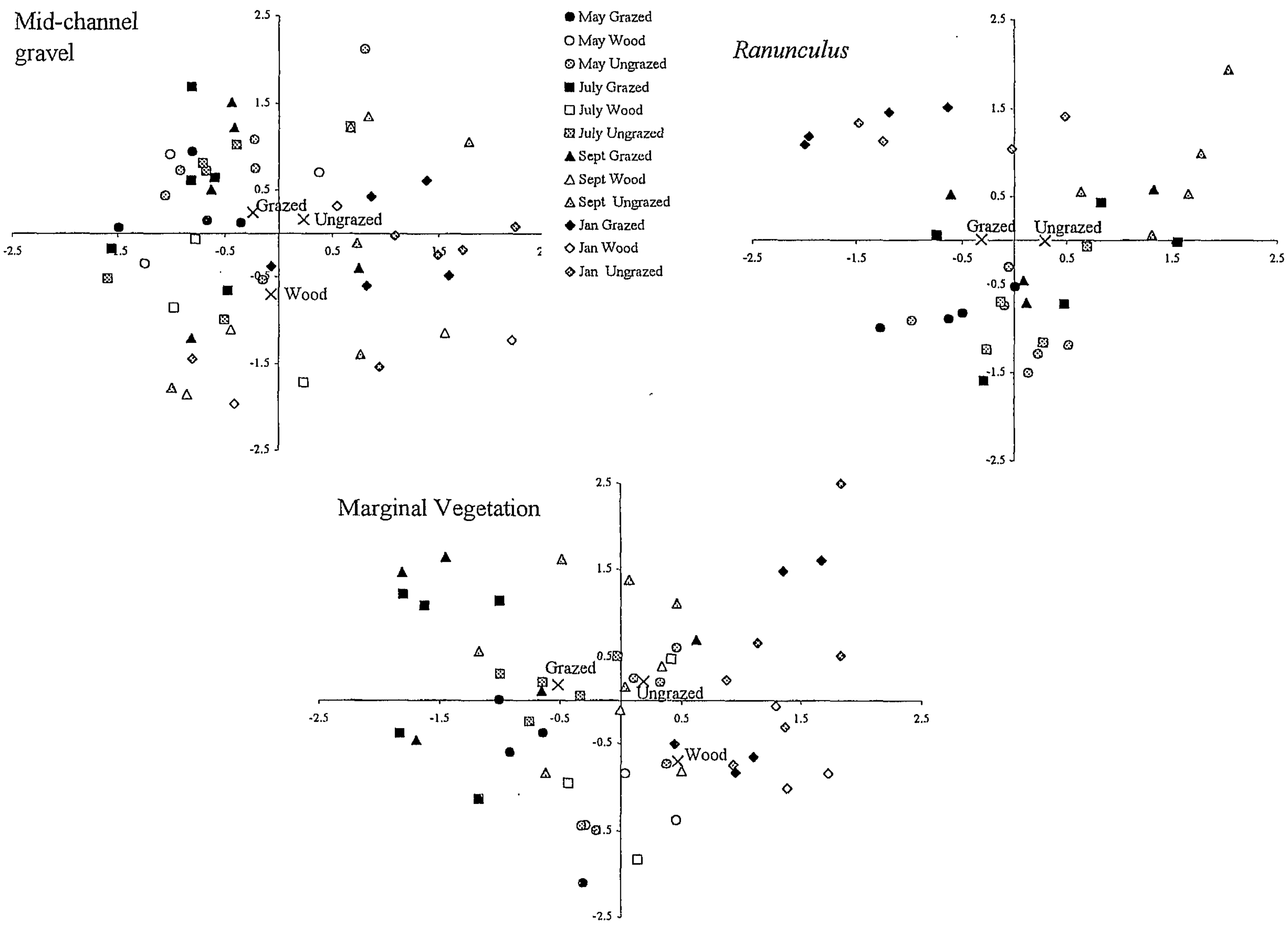
Sample scores along the first two axes of the principal components analysis (PCA) on log-transformed family abundance data, for each habitat, are shown in Fig. 3.2. The cumulative percentage variation explained by the first four axes and the eigenvalues of each axis are shown in Table 3.1. Eigenvalues are the maximised dispersion of taxon scores along each ordination axis and are thus a measure of the importance of each ordination axis. The first axis of the ordination has the largest eigenvalue, the second axis has the second largest eigenvalue etc. Eigenvalues lie between 0 and 1. Values over 0.5 denote a good separation of taxa along axes.

The plots of sample scores along the first two ordination axes, indicated that most of the variation between samples from each habitat was accounted for by differences between seasons, rather than management type (Fig. 3.2). The mean values of sample scores for each management type, plotted on the ordination diagrams for each habitat, showed little separation, and were clustered around the intersection of the two axes (Fig. 3.2). The first two axes of the principal components analysis explained only 24.4%, 44.9% and 26.9% of the variation between samples from mid-channel gravel, *Ranunculus* and vegetated margins, respectively (Table 3.1). The low eigenvalues of these first two axes (all less than 0.3) indicated that there was little difference between samples along any gradient (Table 3.1).

Table 3.1. Eigenvalues along each of the first four axes of the PCA and cumulative percentage variance of data explained by each of the first four axes. Samples were log-transformed abundance data of families from three habitats (gravel, *Ranunculus* and vegetated margins) across different stretches ('grazed', 'ungrazed', 'woodland') and four months (May, July, September and January).

	Axis 1	Axis 2	Axis 3	Axis 4
Mid-channel Gravel				
Eigenvalues	0.125	0.119	0.092	0.080
Cumulative percentage variance explained by axis	12.5	24.4	33.6	41.6
Ranunculus				
Eigenvalues	0.290	0.159	0.083	0.074
Cumulative percentage variance explained by axis	29.0	44.9	53.2	60.6
Marginal vegetation				
Eigenvalues	0.152	0.117	0.103	0.077
Cumulative percentage variance explained by axis	15.2	26.9	37.2	44.9

Fig. 3.2: Plot of sample scores along the first two axis of a Principal Components Analysis. Samples are log-transformed abundance of invertebrate families from each habitat (mid-channel gravel, *Ranunculus* and vegetated margins) in grazed, ungrazed and woodland management regimes, in May, July, September and January. The mean scores of samples from each management regime are shown.



A 1-way ANOVA performed on sample scores along the first ordination axis showed that management type was a significant factor for vegetated margins only (Table 3.2). Sample scores from 'Grazed' margins were significantly different from both 'Ungrazed' and 'Woodland' margin scores. 1-way ANOVAs performed on sample scores along the first ordination axis with season as main factor showed that season was highly significant, for each habitat.

Table 3.2. Results of 1-way ANOVAs performed, for each habitat, on differences between scores of the first axis of the Principal Components Analysis with Management type and Season as main factors. Differences between individual stretch types or seasons were tested with pair-wise Tukey/Kramer *a posteriori* tests. * = P < 0.05

Habitat	Factor	dF	F-Ratio	P	Significant differences (P<0.05) between pairs of management types or seasons
Mid-channel Gravel	Management type	2,54	1.182	0.315	
	Season	3,54	12.293	< 0.001*	May vs Sept, May vs Jan, July vs Sept, July vs Jan, Sept vs Jan
Ranunculus	Management type	1, 35	3.444	0.072	
	Season	3, 35	9.642	< 0.001*	May vs Sept, May vs Jan, July vs Jan, Sept vs Jan
Vegetated Margins	Management type	2,53	4.690	0.014 *	Grazed vs Ungrazed, Grazed vs Woodland
	Season	2,53	27.024	< 0.001*	May vs July, May vs Jan, July vs Jan, Sept vs Jan

3.3.4 Classification of communities in each habitat across different management types and season.

Cluster analysis of the invertebrate communities from each habitat across seasons and management types, showed that, as for the ordination, communities separated mainly across season, rather than management type (Fig. 3.3). For mid-channel gravel communities, the first TWINSPAN division largely distinguished between samples from January and those from other months (Fig. 3.3) September samples appeared on both sides of the dichotomy, whereas May and July samples were on one side only. The second level of classification failed to distinguish between samples from season or management type. For *Ranunculus* communities, the first TWINSPAN division distinguished mainly between samples from September and those from May, although September samples were not as completely classified as those from May (Fig. 3.3). Samples from January and July were on both sides of the dichotomy. The second level of classification failed to distinguish between samples from season or management type, as for gravel. For communities from vegetated margins, the first TWINSPAN division distinguished between samples from January, but not other months (Fig. 3.3). Most samples from grazed stretches were also distinguished at this level, although both sides of the dichotomy had some samples from all management types. The second division did not distinguish between management type or season.

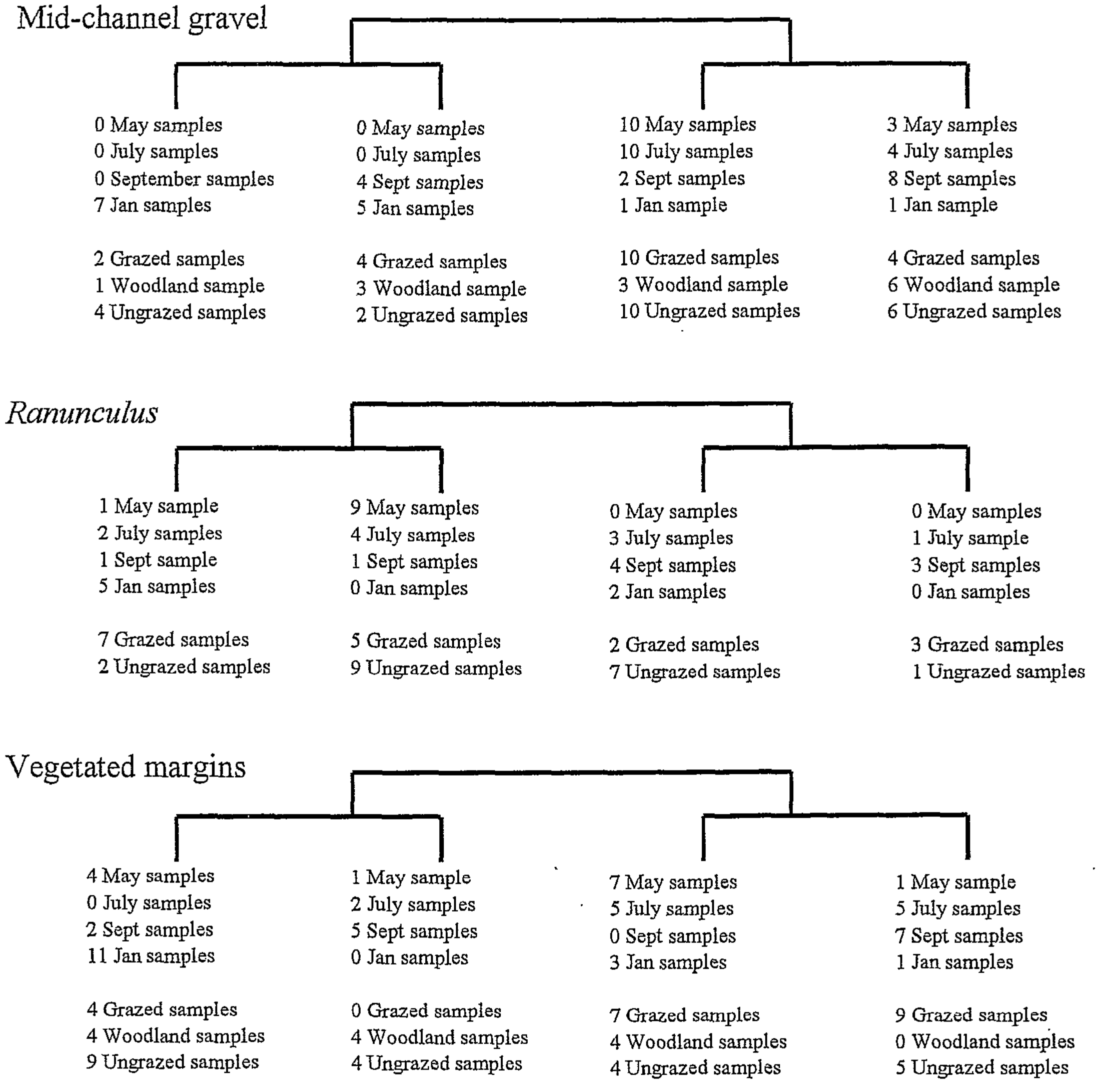


Figure 3.3. Hierarchical cluster analysis of log-transformed invertebrate family abundance data using TWINSPAN. Samples were taken from mid-channel gravel from six streams, three management types ('grazed', 'ungrazed' and 'woodland') and across four sampling periods, May, July, September and January.

3.3.5 Difference in abundance of individual families between stretches

Despite the small differences between invertebrate communities between stretches, there were significant differences in the abundance of individual families. (The families encountered in the investigation are shown in Section 3.3.1 b). Families with significant differences in abundance between stretches of different management type are shown in Table 3.3. As for physical differences, abundance of families was compared between ungrazed and grazed stretches (5 streams) and between ungrazed and woodland stretches (3 streams).

Table 3.3. Families showing significant differences in mean abundance per sample between 'ungrazed' and 'grazed' stretches in each of three habitats, Gravel, *Ranunculus* and Vegetated margins. * = P<0.05, + = P<0.1 M J S J = May, June, September, January (respectively)

Families	UNGRAZED STRETCHES												GRAZED STRETCHES											
	Gravel				*Ranunculus*				Margin				Gravel				*Ranunculus*				Margin			
	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J
Brachycentridae									+															
Hydroptilidae	+	*							*			+												
Hydropsychidae		+						+			+	+												
Leptoceridae							*		+															
Lepidostomatidae											*													
Odontoceridae			*																					
Sericostomatidae		*										+												
Rhyacophilidae										+							*							
Elmidae		*	*		*		*		+		+	+												
Dytiscidae			*			*																		
Hydraenidae											+													
Caenidae	+		*	+																				
Baetidae												*										+		
Heptageniidae			*	*					+			+												
Leptophlebiidae																								*
Leuctridae											+													
Calopterygidae									*	*	*	*												
Ancylidae				*				+																
Bithyniidae																							*	
Lymnaeidae				*																				*
Hydrobiidae								*																
Valvatidae																			+					
Planorbidae																								*
Erpobdellidae																*								
Glossiphoniidae													+		+									
Asellidae							*				*													
Gammaridae					*																			
Ostracoda	*																							
Nepidae																						*		
Veliidae																					*			
Ceratopogonidae																					*			
Tipulidae											*												+	
Simuliidae										*	*													
Tanypodinae								+																
Empididae																								+
Sialidae										+														
Hydracarina				*																				+
Tricladida			*						+															
Gasterosteidae																							*	
Cottidae																					+			
Total abundance																						+		
Numbers of families Showing significant differences (P<0.05)	12				6				7				1				1				8			
Numbers of families Showing significant differences (P<0.1)	15				9				20				2				2				13			

a) Differences between grazed and ungrazed stretches

There was a greater number of families that were significantly more abundant in ungrazed stretches than there were in grazed stretches for mid-channel gravel and *Ranunculus* habitats (Table 3.3). Similar numbers of families were significantly more abundant in ungrazed and grazed stretches in vegetated margins. Particular families that showed strong differences between stretches included the Hydroptilidae and Hydropsychidae (caddis), the Elmidae (beetles), Caenidae and Heptageniidae (mayflies) and Calopterygidae (damselflies). The Hydropsychidae and Elmidae were more abundant in ungrazed stretches for all three habitats. The Hydroptilidae and Heptageniidae were more abundant in ungrazed stretches for both gravel and margins. The Caenidae were more abundant in ungrazed stretches in gravel only, and the Calopterygidae were more abundant in ungrazed stretches in margins only. As a group, the caddis were almost always more abundant in ungrazed stretches, again across all habitats. Families of snails and water-bugs were typically more abundant in grazed margins. Total abundance showed little difference between stretches and was only weakly significantly greater in grazed vegetated margins. Taxon richness within the major orders of invertebrates was greater in ungrazed stretches (Table 3.4), across all habitats. Total diversity was significantly greater only in ungrazed vegetated margins in January.

Table 3.4. Significant differences in taxon richness per sample within the dominant invertebrate orders between 'ungrazed' and 'grazed' stretches in each of three habitats, Gravel, *Ranunculus* and vegetated margins. * = P<0.05, + = P<0.1. M J S J = May, June, September, January.

Families	Ungrazed Stretches												Grazed Stretches											
	Gravel				*Ranunculus*				Margin				Gravel				*Ranunculus*				Margin			
	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J
Trichoptera												*					+							
Coleoptera			*		+		*																	
Hemiptera																								
Mollusca					*	+																		
Diptera																								
Ephemeroptera			+		+		*					*												
Total taxon richness												*												

b) Differences between ungrazed and woodland stretches

There was little difference in the number of families in mid-channel gravel that were significantly more abundant in ungrazed stretches and those more abundant in woodland stretches (Table 3.5). However, there were more families that were more abundant in ungrazed margins compared to woodland margins. The Elmidae were particularly more abundant in woodland gravel. These, together with the Tanypodinae, were the only groups that showed a significantly greater abundance in one stretch type in more than one month. The total abundance was only weakly significantly more abundant in ungrazed stretches, for one month only in both gravel and margin habitats (Table 3.5).

Table 3.5. Families showing significant differences in mean abundance between 'ungrazed' and 'woodland' stretches in each of two habitats, Gravel and Marginal Vegetation.
* = $P<0.05$, + = $P<0.1$ M J S J = May, June, September, January (respectively)

Families	UNGRAZED STRETCHES								WOODLAND STRETCHES							
	Gravel				Margin				Gravel				Margin			
	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J
Glossosomatidae										*						
Limnephilidae															+	
Rhyacophilidae		+														
Ephemerellidae		+				+										
Caenidae	*					+										
Heptageniidae									*							
Ancylidae					+											
Lymnaeidae		*												*		
Physidae							*									
Planorbidae							*									
Elmidae									*	*		+				
Helodidae																+
Gyrinidae								+								
Veliidae														*		
Asellidae								+								
Stratiomyiidae													+			
Tanypodinae						+	*									
Hydracarina						*										
Total abundance	+					+										
Numbers of families Showing significant differences ($P<0.05$)	2				4				3				2			
Numbers of families Showing significant differences ($P<0.1$)	4				9				3				5			

Taxon richness within the major orders of invertebrates was greater in ungrazed margins for Coleoptera, Hemiptera and Mollusca (Table 3.6). Only Mollusca were weakly significantly more diverse in ungrazed gravel. No orders were more diverse in woodland stretches. Total diversity was not significantly greater in either management type.

Table 3.6. Significant differences in taxon richness per sample within the dominant invertebrate orders between 'ungrazed' and 'woodland' stretches in Mid-channel gravel and Vegetated margin habitats. * = $P<0.05$, + = $P<0.1$. M J S J = May, June, September, January (respectively)

Families	Ungrazed Stretches								Woodland Stretches							
	Gravel				Margin				Gravel				Margin			
	M	J	S	J	M	J	S	J	M	J	S	J	M	J	S	J
Trichoptera																
Coleoptera								*								
Hemiptera								*								
Mollusca		+						*								
Diptera																
Ephemeroptera																
Total taxon richness																

3.3.6 Differences in abundance per sample of *Agapetus fuscipes* larvae in the three stretch types

The abundance of *Agapetus fuscipes* larvae in each stretch type for the three streams with woodland stretches, is shown in Table 3.7. The numbers in woodland reached a very high density in July and September, particularly in the Bere and Middle Piddle. There was very low persistence of larval populations in both these streams. Larvae were virtually absent from September onwards in the Bere stream and from January in the Middle Piddle. Numbers were more stable in the Tadnoll brook.

Table 3.7. Numbers of *Agapetus fuscipes* per sample (mean of three samples) in each stretch type over the four sampling occasions. B = Bere stream, MP = Middle Piddle, T = Tadnoll brook.

Month	Grazed stretches			Ungrazed stretches			Woodland stretches		
	B	MP	T	B	MP	T	B	MP	T
May	2.2	0	-	1.1	0.7	0	0	21.5	2.2
July	17.7	2.2	-	6.5	10.8	2.2	286.3	1196.7	35.0
September	0	6.5	-	0	6.8	0	0	953.3	21.7
January	2.2	0	-	0	9.0	0	0.3	0	17.3

3.3.7 Difference in abundance and diversity of Adult aquatic insects in terrestrial vegetation between stretches

a) Differences between grazed and ungrazed stretches

Sweep samples of adults were taken in May, July and September. There were significant differences in the abundance of adult insects caught in terrestrial vegetation between the two management types (Fig. 3.4, top panel). Adults of all the major orders were found in greater abundance in ungrazed vegetation. Trichoptera in particular were more abundant in ungrazed vegetation, differences being significant for each month. The total abundance of adult insects was significantly greater in ungrazed stretches in July. The diversity of adult families of the major orders was also greater in ungrazed stretches. Again, this was true particularly of caddis adults, which were significantly more diverse in both July and September (Fig. 3.5, top panel).

b) Differences between Ungrazed and Woodland stretches

Adult Trichoptera and Diptera were significantly more abundant in woodland vegetation, though only on one of the three sampling occasions (Fig. 3.4, lower panels). Abundance of adult Ephemeroptera showed little difference between stretches. The total abundance of adults was significantly greater in woodland stretches, in July. The diversity of Trichoptera and Diptera families was greater in woodland stretches compared to ungrazed stretches, in both July and September. Total family diversity was also greater in July and September (Fig. 3.5, lower panel).

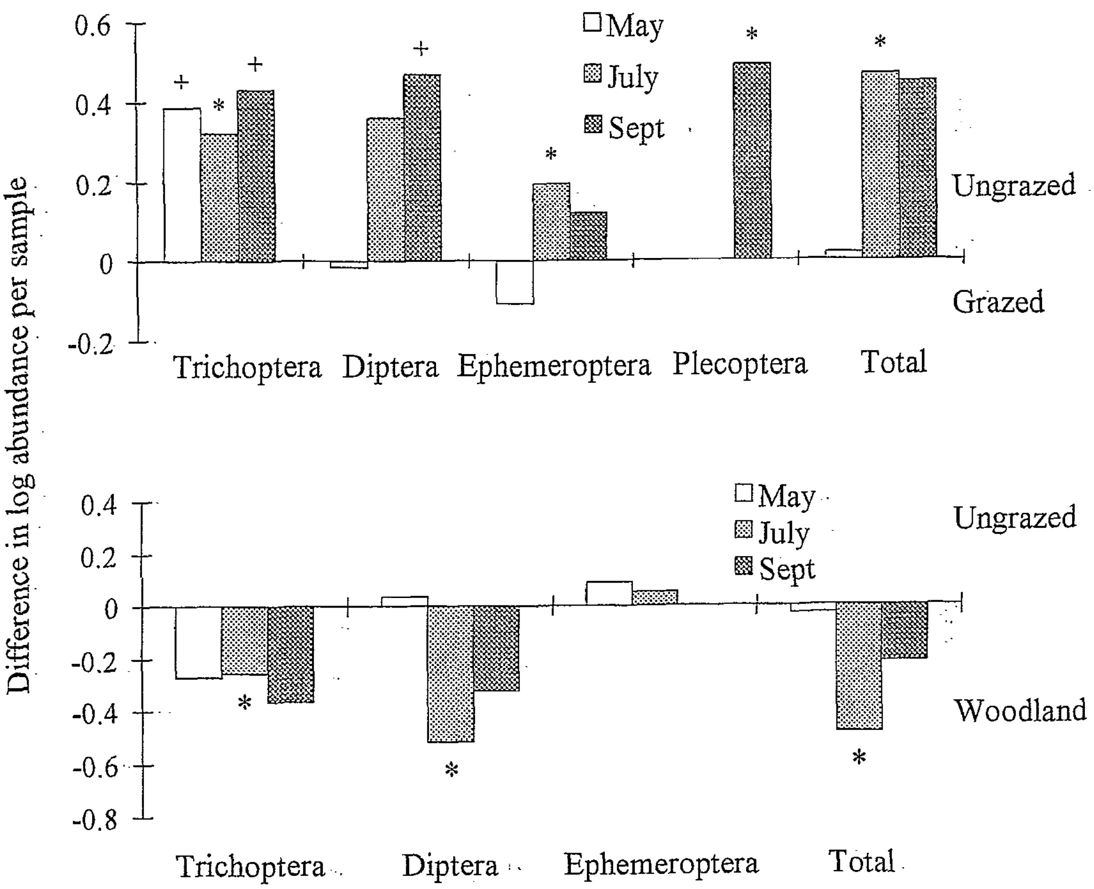


Figure 3.4.

a, top panel) Mean difference in total abundance per sample (log-transformed) of adults of the major groups of aquatic insects caught in sweeps of 'grazed' and 'ungrazed' bankside vegetation.
* = P<0.05, + = P<0.1

b) Mean difference in total abundance per sample (log-transformed) of adults of the major groups of aquatic insects caught in sweeps of 'woodland' and 'ungrazed' bankside vegetation.
* = P<0.05, + = P<0.1

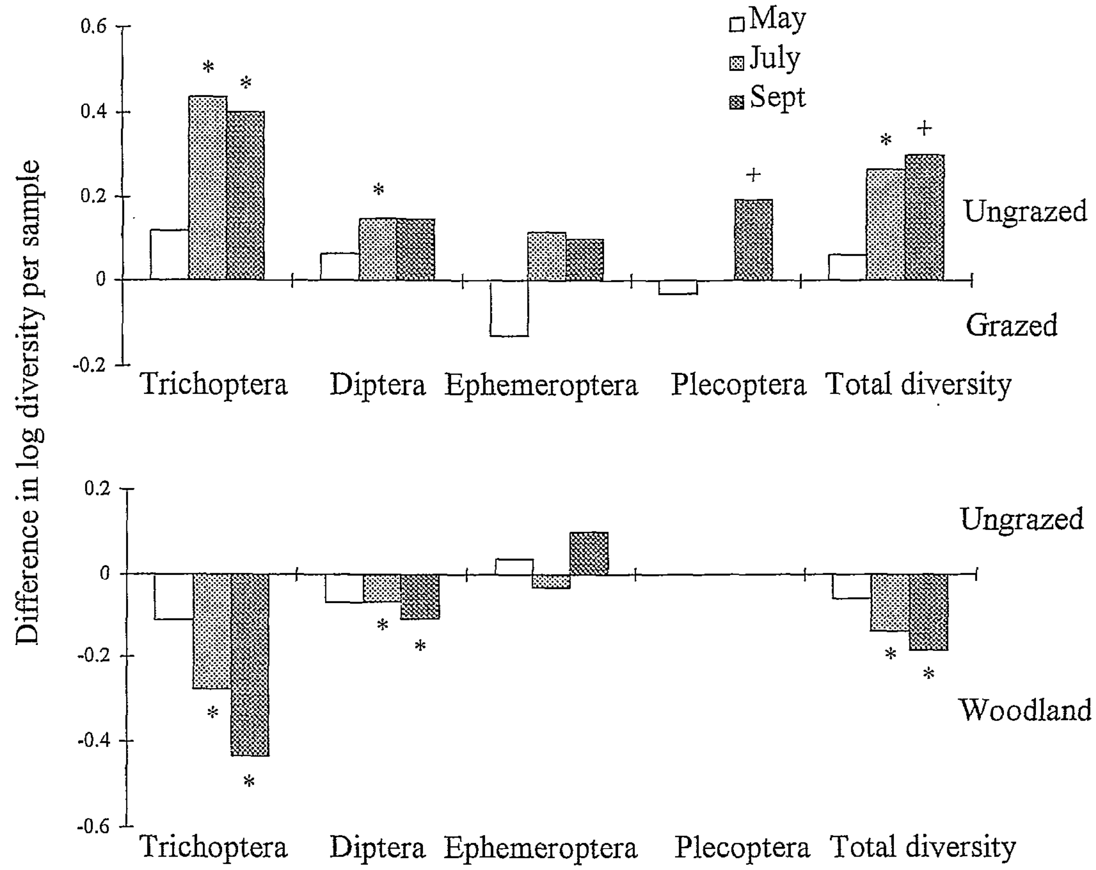


Figure 3.5.

a) Mean difference in diversity/richness per sample (log-transformed) of adults of the major groups of aquatic insect caught in sweeps of 'grazed' and 'ungrazed' bankside vegetation
* = P<0.05, + = P<0.1

b) Mean difference in diversity/richness per sample (log-transformed) of adults of the major groups of aquatic insect caught in sweeps of 'ungrazed' and 'woodland' bankside vegetation
* = P<0.05, + = P<0.1

It is important to remember at this point that only certain ungrazed reaches were used for analysis with grazed and woodland reaches. Comparisons were only made between management types where they occurred on the same stream – thus woodland could not be compared to grazed because only 2 sites were found where both regimes were adjacent. The number of ungrazed sites sampled was actually higher overall than the number of wooded or grazed areas, hence it appears (Table 3.8) that ungrazed stretches support more diverse adult-invertebrate communities overall than either 'grazed' or 'woodland'. Clearly the more samples that are collected the higher the abundance and diversity will be. Same-stream comparisons of different regimes, however, demonstrate that woodland areas support a more diverse and abundant emergent-adult community than ungrazed, and ungrazed areas are similarly well 'stocked' compared to grazed (Figures 3.4 & 3.5).

Table 3.8, showing the distribution and diversity of the main adult invertebrate taxa caught in sweep-net samples, on three sampling occasions (May, July and September 1996), for all grazed, ungrazed and woodland sites combined.

	Grazed			Ungrazed			Wood		
	May	July	Sept.	May	July	Sept.	May	July	Sept.
Agapetus	✓	✓	✓	✓	✓	✓	✓	✓	✓
Leptoceridae				✓	✓	✓	✓	✓	✓
Odontoceridae				✓	✓				
Rhyacophilidae				✓	✓			✓	
Hydroptilidae	✓	✓	✓	✓	✓	✓	✓		✓
Hydropsychidae				✓	✓		✓	✓	
Sericostomatidae	✓			✓	✓		✓	✓	
Goeridae	✓			✓	✓	✓		✓	
Limnephilidae				✓		✓			✓
Psychomyiidae						✓	✓	✓	
Beraeidae							✓		
Psychodidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ceratopogonidae	✓	✓		✓	✓	✓	✓	✓	✓
Chironomidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Empididae	✓		✓	✓	✓	✓	✓	✓	✓
Culicidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Simuliidae	✓		✓	✓	✓	✓	✓	✓	✓
Tipulidae	✓	✓	✓	✓	✓	✓	✓	✓	✓
Ptychopteridae							✓		
Stratiomyiidae		✓			✓			✓	
Baetidae	✓			✓	✓		✓	✓	
Caenidae				✓					
Ephemerellidae	✓	✓	✓	✓	✓	✓	✓		
Leptophlebiidae	✓	✓		✓				✓	✓
Ephemeridae	✓	✓		✓			✓		
Heptageniidae				✓					
Nemouridae	✓			✓					
Perlodidae	✓			✓					
Leuctridae						✓			✓
Sialidae	✓			✓					
Agrion splendens				✓					

3.4 Discussion

3.4.1 Differences in invertebrate communities between grazed and ungrazed stretches

Little difference in overall invertebrate community composition was seen between grazed and ungrazed stretches in either mid-channel gravel or *Ranunculus* habitats. This reflected the similarity of structure and physical conditions in each habitat across the two stretch types. Invertebrate communities from the margins showed more differences between stretch types, however. Due to the trampling action of cattle at the water's edge, the physical profile of grazed margins was different from that in ungrazed stretches. Grazed margins typically had wider expanses of shallow, silty 'pondlets', and few overhanging, trailing stems and leaves from terrestrial vegetation. Significantly more snails, true bugs and small fish were found in these grazed margins. This may have been due to the greater growth of algal food for snails, better hunting conditions for bugs (due to a greater expanse of still, open water) and energetically 'better' habitats for young fish (Garner *et al*,. 1998). Although possessing similar invertebrate communities, both mid-channel gravel and *Ranunculus* had significant differences between stretches in the abundance of several families. These family differences are likely to be due to a suite of abiotic and biotic factors, both aquatic and terrestrial.

Consistent differences in physical aquatic conditions between stretch types, other than local light levels, are likely to have been slight, due partly to the short length of each stretch type (frequently only a field's length long – approx. 50m) as the streams flowed through the agricultural landscape. Groundwater-fed chalk streams also exhibit considerable independence from terrestrial riparian conditions, especially in terms of temperature, substrate or flow rate, as these latter are determined largely by aquifer conditions, distance downstream from source and gradient (Mann *et al.*, 1989; Mackey & Berrie, 1991; Berrie, 1992; Ladle & Westlake, 1995). Flow conditions and substrate type also exhibited greater variability within stretches and between the six streams studied than between stretches. In addition, habitats were sampled in such a way as to minimise variation between stretch types. The amount of organic debris in all stretches of chalk streams is likely to be high due to decay of both in-stream macrophytes and to terrestrial input (Dawson, 1976). Again within-stretch and between-stream differences in organic debris are likely to have been greater than between-stretch differences.

Biotic influences in the aquatic environment included the presence of the brown trout (*Salmo trutta*), which are voracious and abundant predators in chalk streams (Mann *et al.*, 1989). They are typically more abundant in stretches with well-developed marginal vegetation and overhanging trees (Sand-Jensen *et al.*, 1989, Giles & Summers, 1996). Brown trout can potentially have large effects on stream invertebrates, particularly on large, conspicuous species (Cooper, 1988; Andersen, 1992; Bechara, *et al.*, 1992; Bechara *et al.*, 1993; Wiseman *et al.*, 1993; Townsend, 1996). Despite the greater abundance of trout in ungrazed stretches, with abundant marginal vegetation (Giles & Summers, 1996), there was little evidence of any effect on either individual or total invertebrate abundance or diversity. Presumably, any effect of greater trout predation (if this occurred) in ungrazed stretches was overridden by other factors.

Marginal vegetation in freshwaters is often reported to possess a greater abundance of invertebrates than other habitats (Westlake *et al.*, 1972; Gregg & Rose, 1985; Schramm & Jirka, 1989; Wright *et al.*, 1994). There are many reasons for this, including the greater algal and plant food availability within macrophyte stands (Sand-Jenssen & Madsen, 1989;

Newman, 1991; Wright *et al.*, 1994; Kornijow *et al.*, 1995) and the greater amount of surface area of substrate available (Soska, 1975; Gregg & Rose, 1985). In addition, macrophytes can provide a critical habitat for certain key life-stages of many taxa, such as pupation, hibernation and egg laying (Glime & Clemmons, 1972; Maurer & Brusven, 1983; Rooke, 1984; Fitter & Manuel, 1986; Richardson & Clifford, 1986). Marginal vegetation may thus act as a 'source' of many species of invertebrate, which then disperse into other, less productive, habitats, such as gravel or *Ranunculus* (Rooke, 1984; Sand-Jenssen *et al.,* 1989). The overall greater abundance of marginal vegetation in ungrazed stretches may therefore be responsible for a greater density of some aquatic taxa that are associated with vegetation (such as Asellidae, Gammaridae, Hydracarina and Ostracoda) in all ungrazed habitats.

Terrestrial differences between stretches were great and were largely due to the differences in vegetation type and physical effects on the bank caused by vegetation growth and stock grazing. These differences would have potentially important influences on the terrestrial life-stages of aquatic insects, including winged adults and pupating or hibernating beetles. Larvae of many of the common caddis families were significantly more abundant in ungrazed stretches, than in grazed stretches (with the exception of the Rhyacophilidae). This was true across all habitats and all six streams. It is unlikely, therefore, that these differences were due to consistent differences in each habitat between the two stretch types. Other insect families that showed a similar significantly greater abundance in ungrazed stretches include the Elmidae, Dytiscidae, Caenidae, Heptageniidae, Simuliidae and, most strikingly, the Calopterygidae (damsel flies). This last family was predominantly the species *Calopteryx (Agrion) splendens.* Large numbers of adults of this species were found among the tall herbaceous vegetation in ungrazed stretches, where they were observed resting, feeding and mating. The greatest influence in the distribution of *Calopteryx splendens* nymphs has been reported to be the complicated territorial requirements of the adults, itself a function largely of riparian vegetation type and structure (Macan, 1962). It is likely, therefore, that the greater abundance of nymphs in ungrazed sections was largely due to localised oviposition by adults, which in turn associated with the tall riparian vegetation in these stretches.

Terrestrial winged adults of all the common orders of aquatic insects (Trichoptera, Diptera, Ephemeroptera and Plecoptera) were more abundant and diverse in ungrazed vegetation, consistent with adult preferences for natural vegetation of high structural and species diversity. Vegetation can act as perching places, swarm markers and can provide refugia from desiccation, wind and predation, for a variety of adult aquatic insects (Downes, 1969; Statzner, 1977; Tozer *et al.*, 1980; Solem, 1984; Welton *et al.* 1987; Jackson & Resh, 1989, Sweeney, 1993). Riparian vegetation can also provide food for adults, to provide energy for flight or ovarian maturation (Jones, 1974; Sweeney, 1993; Petersson & Hasselrot, 1994). Riparian vegetation type and structure has been found to be a major factor in the distribution and abundance of adult caddis and Odonata along streams (Ormerod *et al.*, 1990; Samways & Steyler, 1996; Collier, Smith & Baillie, 1997).

These results are consistent with the hypothesis that the terrestrial habitat in ungrazed stretches favoured the adults of several families of aquatic insect, which in turn oviposited eggs in these stretches, rather than in grazed stretches with poorly developed bankside vegetation. Larvae of these families, which presumably did not significantly re-distribute away from oviposition sites, were thus found in greater abundance in ungrazed stretches. For many taxa which oviposit eggs on the water surface, or whose larvae drift rapidly away from centres of oviposition, adult distribution will have little effect on larval distribution, due to the rapid re-distribution of early instars in the drift.

Very few studies have looked at the potential link between adult habitat suitability and the abundance and distribution of larvae, although this area is now attracting greater attention from stream biologists (e.g. Collier *et al.*, 1997; Collier & Smith, 1998). Anecdotal accounts have often described the dependence of larval aquatic insects on adult oviposition choice. Macan (1961) stated that 'a species may be absent from a place because conditions, though not unfavourable, are not attractive to the ovipositing female'. Recent work on the genetic variability of caddis populations has shown that larval caddis within 50-100m reaches are closely related, and are the result of oviposition by relatively few females, coupled with limited dispersal away from oviposition sites (Bunn & Hughes, 1997). Adult oviposition location and success thus largely determined the abundance and distribution of larvae at small scales. Adult preferences for riparian vegetation types has been shown to influence the distribution and abundance of lake littoral caddis and chironomid larvae (Harrison & Hildrew, 1998) and lotic caddis larvae (Statzner, 1977).

The strikingly greater abundance of elmid beetles in ungrazed stretches cannot be accounted for by differences in habitat (e.g. differences in flow rate or substrate), as they were more abundant in all ungrazed habitats. Elmid beetles pupate in protected sites above the water line on the terrestrial bankside, where they need moist, well-structured soils (Brown, 1987). Larvae have also been found in bankside soil well above the water line, where they were possibly looking for suitable pupation sites (*Pers. obs.*). The management of banksides, particularly with respect to vegetation, will influence the physical nature of the soil. Grazed and poached banksides will tend to have poorly structured soils that become either waterlogged and anoxic in wet weather or hot and dry in dry weather. This may well be unfavourable for beetle pupation and thus interrupt the life histories of beetles in grazed stretches, resulting in lower density in all habitats. The same mechanism may also operate for other beetle families (such as the Dytiscidae), which are also reported to pupate in damp bankside soils (Fitter & Manuel, 1986). The influence of bankside management on beetle pupation success has been hitherto almost completely ignored in freshwater ecology, yet may be critical for many beetles, including rare or endangered species.

3.4.2 Differences in invertebrate communities between ungrazed and woodland stretches

The relatively low number of replicate streams where it was possible to compare woodland and ungrazed stretches meant that fewer taxa showed significant differences between stretches. Where taxa occurred in all three streams, there were fewer differences than might be expected, given the often-reported reduction of primary and secondary production in shaded stream stretches (Hawkins *et al.* 1982; Behmer & Hawkins, 1986; Dudgeon & Chan, 1992; Reed *et al.*, 1994). Total abundance per sample in each habitat was only marginally greater in ungrazed stretches, demonstrating the weak effect of woodland shading on invertebrate secondary production in the gravel and margins, in these short stretches of chalk streams. *Ranunculus* patches in woodland were not sampled due to their scarcity, and thus no comparisons can be made for this habitat. However, with respect to habitat diversity, small patches of *Ranunculus* in woodland may contribute relatively more 'value' than large *Ranunculus* stands in ungrazed areas. Lack of satisfactorily comparable woodland *Ranunculus* patches prevented this from being assessed though. Overall secondary production in woodland would thus have been considerably lower than in open stretches, due to a lack of habitat rather than to lower food levels. It is possible that the relatively large amounts of detritus from decaying macrophytes partially compensated for the lack of primary production in heavily shaded sites. In addition, algal quality may have been higher per unit biomass in shaded sites, due to a relatively greater concentration of chlorophyll in shaded cells. Drift of invertebrates into woodland sections from upstream could also have replenished populations of lower density. Two families in particular were significantly more abundant in woodland gravel, compared to gravel in ungrazed (sunlit) stretches, although both are reported to eat periphyton and other plant-based material. Glossosomatid caddis larvae (almost all *Agapetus fuscipes*) were extremely abundant in woodland gravel in July, although numbers declined rapidly in September and January. Elmid beetles (largely *Limnius volckmari*) were also much more abundant in woodland gravel.

For both families (Glossosomatidae and Elmidae), the greater densities of the aquatic stages in woodland gravel may be due to two factors. Either aquatic conditions were more suitable there (for example, fractionally lower temperatures or more of a certain kind of food), or terrestrial conditions for the winged adult caddis and the pupating stages of the beetle were more favourable in woodland. The higher numbers and diversity of adult Trichoptera and Diptera found in woodland indicated that short stretches of tree cover both sides of the stream present a superior habitat for many adults of these two groups, compared to more open areas, even those with abundant vegetation. The higher humidity, lower wind speeds and particularly lower air temperatures in woodland environments may all enhance adult survival and longevity (Collier *et al.*, 1997). Larval conditions in woodland are unlikely to have been much more favourable for *Agapetus fuscipes* as primary productivity would have been lower in the shaded woodland stretches and the larvae are reported to feed largely on benthic diatoms and detritus (Castro, 1975). In addition, the exceedingly high recruitment followed by population collapse shortly afterwards, indicated that larval persistence in woodland was very low, possibly due either to larval dispersal away from woodland towards sites of greater productivity, or to high mortality. A further intensive investigation on this species has found that adults oviposit under or near trees and that the larvae drift downstream as they grow. High numbers of larvae in woodland thus probably reflected adult habitat choice, rather than larval choice (Harrison *et al.*, in prep.)

Elmid beetles may be more abundant in woodland because of the superior riparian conditions for pupation in the soil. Woodland soils are likely to be well-structured and aerated, due to the presence of abundant tree roots, and also permanently moist and cool, relative to soils in more open areas. Larvae and pupae of *Limnius volckmari* were found in the soil of the woodland banks, although no quantitative samples were taken. This almost completely ignored subject needs further investigation.

Native Crayfish

Three native crayfish (*Austropotamobius pallipes*) were observed during the sampling programme. This species is protected under the Wildlife & Countryside Act (1981), included in the IUCN Red Data List, and listed under Annex 2 of the Habitats Directive (92/43/EEC). Although the animals were too rare to support objective analysis, details of the discoveries are provided:

	Watercourse	Month	Section	Habitat
1)	Tadnoll Brook (Frome trib.)	July	Ungrazed	Marginal overhanging vegetation
2)	River Piddle (lower section)	July	Ungrazed	Marginal reeds
3)	Bere Stream (Piddle trib.)	September	Woodland	Marginal overhanging vegetation

It would be precipitate to assign a habitat preference to this animal based on this evidence, however marginal vegetation in ungrazed reaches would appear to play a very important role in its distribution. A survey by the Game Conservancy Trust also showed that native crayfish are more abundant in sections of the Piddle where there is no grazing. Cattle-trampling, adverse abiotic conditions and predation by birds in the open, grazed areas may all contribute to this distribution.

3.5 Conclusions

Although there was little difference in overall invertebrate density between stretches of different management type, there was significantly greater diversity in the ungrazed stretches, than either woodland or grazed stretches. This probably reflects the greater diversity of both aquatic and terrestrial habitat in the former. The value of such short sections of 'unmanaged' stream bankside to stream biodiversity is therefore considerable. The greater abundance of terrestrial adults in ungrazed and woodland sections, as streams ran through the mixed agricultural landscape, reflects the importance of natural riparian vegetation to adult stages, and thus to the 'supply' of new aquatic insect recruits. Woodland stretches, in particular, although having lower primary and secondary production, may act both as important generators of new recruits (such as *Agapetus fuscipes* larvae) to more open stretches, and as refugia for adults which then disperse and oviposit in open stretches.

Streams without such natural bank vegetation, as may be found in areas of intensive upland grazing or lowland agriculture, may have a less-diverse invertebrate fauna as a result. The paucity of riparian vegetation over wide areas may also reduce the recruitment of new larvae. Increased understanding of the relationship between adult habitat requirements in the riparian zone and management of bankside vegetation will greatly assist in restoration and planting schemes for river corridors (Collier & Smith, 1998).

The re-connection of degraded river sections with more natural sections, in order to allow re-colonisation of organisms throughout fluvial landscapes (Stanford *et al.*, 1996) will also require knowledge of how adults disperse along banks, and in particular how banks denuded of vegetation may present a barrier to adult longitudinal dispersal.

3.6 Summary

- Semi-quantitative invertebrate samples were taken from three habitats: mid-channel gravel, *Ranunculus* and marginal vegetation – in six lowland chalk streams, on four sampling occasions spread between May 1996 and January 1997. Samples were taken from stream stretches with three different types of management regime:

1. Grazed stretches fully accessible to grazing cattle and which had simple, grassy margins,
2. Ungrazed stretches fenced from stock, that had abundant and diverse marginal vegetation,
3. Woodland stretches that had abundant riparian trees but only sparse marginal vegetation.

- Little difference was found in overall invertebrate community between habitats from different stretch types, reflecting the similar physical conditions in each habitat across stretches. However, there were significant differences in the abundance of certain families between stretch types.

- A greater number of invertebrate families were more abundant in habitats in ungrazed stretches compared to the same habitats in grazed stretches. This was particularly the case for caddis families, elmid and dytiscid beetles, caenid and heptageniid mayflies and calopterygid damselflies.

- Taxon diversity was higher in ungrazed habitats, compared to grazed habitats. Differences between the two stretch types could be explained by the more abundant and diverse marginal vegetation in ungrazed stretches, which may have acted as a possible 'source' of invertebrates to other habitats.

- A similar number of families were more abundant (as larvae) in habitats in ungrazed compared to woodland stretches, despite the lower abundance of marginal macrophytes in woodland. There was greater taxon diversity within certain orders of invertebrate in ungrazed, compared to woodland stretches. Two families were, however, particularly more abundant in woodland gravel, compared to gravel in ungrazed stretches – glossosomatid caddis and elmid riffle beetles.

- A greater abundance and variety of terrestrial adult aquatic insects were caught in bankside vegetation along ungrazed stretches, compared to grazed stretches. This may have increased the reproduction and local recruitment of aquatic insects in these stretches.

- However, the terrestrial adult abundance and species-richness was greater in woodland compared to ungrazed stretches, indicating that dense riparian trees also provide a valuable habitat or refuge to adults of many aquatic insect species, and possibly provide a superior adult habitat compared to more open banksides. Elmid beetles may also favour wooded banksides as sites of pupation.

- Management of riparian corridors along chalk streams should ensure a high diversity of bankside vegetation. Extensive stretches of heavily grazed banks should be avoided and stretches with abundant 'untidy' marginal and terrestrial vegetation encouraged. Short stretches of woodland bankside, although reducing primary and secondary production and lowering in-stream diversity, may act as vital areas of adult habitat, thus increasing reproduction and recruitment in streams with proximate wooded areas.

4. THE FUNCTIONAL ECOLOGY OF AQUATIC MARGINS

4.1 Introduction

Much research in running waters over the last three decades has focused on the biotic and abiotic factors that explain the distribution and abundance of aquatic invertebrates (Rabeni & Minshall, 1977; Minshall, 1984; Statzner & Higler, 1986; Power *et al.*, 1988). A recent applied area of lotic invertebrate ecology has sought to classify into distinct 'biotopes' or habitats, areas or patches of similar physical and biological properties (Palmer *et al.*, 1991; Harper *et al.*, 1992; Armitage *et al.*, 1995; Harper *et al.*, 1995). Such discreet habitats can be defined by their similar invertebrate assemblages (Pardo & Armitage, 1997). Knowledge of invertebrate-habitat associations can facilitate more accurate monitoring and assessment of running water invertebrates, as representative samples can be taken of all invertebrate communities, from the various habitats identified in any particular water body. Such habitats can also be used as the 'building blocks' of conservation or restoration efforts in streams and rivers (Harper *et al.*, 1992). In this approach, managers can focus on aquatic habitats in damaged or restored stream sections to ensure they are not under- or over-represented, compared to natural, unaltered water courses. Although much research has been undertaken to identify and classify in-stream aquatic habitats with respect to their macroinvertebrate assemblages, relatively little attention has been focused on the vegetated margins as a distinct habitat (Harper *et al.* 1995; Newson *et al.*, 1998). There is a growing awareness, however, that the 'conservation value' of this habitat can be high relative to other habitats in the stream. This is due in part to the apparent high macroinvertebrate diversity associated with emergent marginal macrophytes and to the 'functional' importance of margins for invertebrates (Ormerod, 1988; Wright *et al.*, 1994; Cogerino *et al.*, 1995; Harper & Everard, 1998).

Lowland chalk streams in the UK typically have extremely stable flows, from their headwaters down to the lower reaches. This stability is due largely to their water being derived from groundwater percolating from chalk aquifers, rather than precipitation-dependent run-off (Berrie, 1992; Ladle & Westlake, 1995). Their physical and chemical conditions and particularly their hydrology is thus determined by groundwater conditions, rather than by short-term rainfall events. As a result, average stream power is low, flood events are rare and there is relatively little lateral erosive force (Westlake *et al.*, 1970; Mann *et al.*, 1989; Berrie, 1992; Ladle & Westlake, 1995). Due to the low erosion and stable water levels, marginal vegetation is abundant along the entire length of most true chalk streams. Headwater streams derived from overland run-off will typically have mineral substrate margins or sparse clumps of marginal vegetation in areas of temporary low erosion. The great abundance and diversity of invertebrates in chalk streams, leading to high conservation status, can, in part, be attributed to the wide diversity of habitats, in particular the abundance of mid-channel and marginal macrophytes (Wright, 1992).

Recent concern about agricultural management practices along chalk streams has focused attention on the functional role that marginal macrophytes play, particularly in the ecology of brown trout (*Salmo trutta*) (Giles & Summers, 1996). Grazing by cattle at the water's edge can have large impacts on chalk stream marginal vegetation, due to the shallow, accessible nature of the banks. Little is known about the functional role such marginal vegetation plays in the ecology of aquatic invertebrates, despite its abundance and ubiquity.

4.2 Methods

4.2.1 Sites

Six small chalk streams were selected for study (Table 2.1, page 4). Each stream was characterised by a coarse gravel substratum, abundant in-stream macrophytes (mainly *Ranunculus* spp.) and marginal vegetation. For a fuller description of chalk streams, see Ladle & Westlake, 1995. There were several different types of marginal vegetation, the occurrence of which depended largely on the nature of riparian management. There were three major types of riparian management regimes: Woodland, Grazed and Ungrazed - see 3.2.2 for a full description.

4.2.2 Sampling regime

Invertebrate samples were taken at the same sites in May, July, September 1996 and January 1997 from three habitats in each stream. These habitats were:

a) mid-channel gravel,
b) *Ranunculus* patches,
c) the various types of marginal vegetation.

Samples were taken as in section 3.2.3, page 19. The captured invertebrates were preserved in alcohol, sorted in the laboratory within three to five months, and counted and identified to the highest possible taxonomic level.

4.2.3 Data Analysis

Data was initially treated in the same manner as in the previous chapter (section 3.2.5). The three samples taken from each habitat (gravel, *Ranunculus* and margin) were combined to give a mean sample for that habitat. This reduced small-scale variations in habitats within a stretch, such as those caused by minor flow changes and different substratum characteristics.

For community analysis, invertebrate samples from the different habitats were ordinated using log-transformed (log x+1) family abundance data. A Principal Components Analysis was used, using the statistical package CANOCO (Ter Braak 1987). Samples were also classified using the TWINSPAN statistical package (Hill, 1979). The TWINSPAN hierarchy was followed to end-groups, which could not be further subdivided.

The abundance of individual taxa in the different habitats (gravel, *Ranunculus* and marginal vegetation), for each sampling occasion, was compared using 1-way ANOVAs on log-transformed data. Post-hoc Tukey-Kramer tests were performed following the ANOVAs to determine significant pair-wise differences between individual habitats. Replicates in the ANOVAs were mean samples from habitats from each of the six streams in which the taxon occurred over the four sampling occasions.

Further community analysis included examining rank abundance data for each habitat, diversity and equitability indices and investigating the relative abundance of all taxa across the three main habitats of gravel, *Ranunculus* and marginal vegetation.

4.3 Results

4.3.1 Differences in invertebrate communities between types of marginal habitats

Community analysis

There were few consistent differences in invertebrate community composition between the different types of marginal habitat (Grazed Grass/*Apium*, Ungrazed reeds, Ungrazed *Apium*, Ungrazed trailing vegetation, Woodland trailing vegetation). A Principal Components Analysis performed on family abundance data (log-transformed) from the different types of margin showed a high degree of overlap in ordination space between samples from different margin types (Fig. 4.1). Eigenvalues were low (Table 4.1). These numbers represent the maximised dispersion of sample scores along each ordination analysis - values over 0.5 denote a good separation of samples along each axis. There was thus only weak separation of samples along the first four axes.

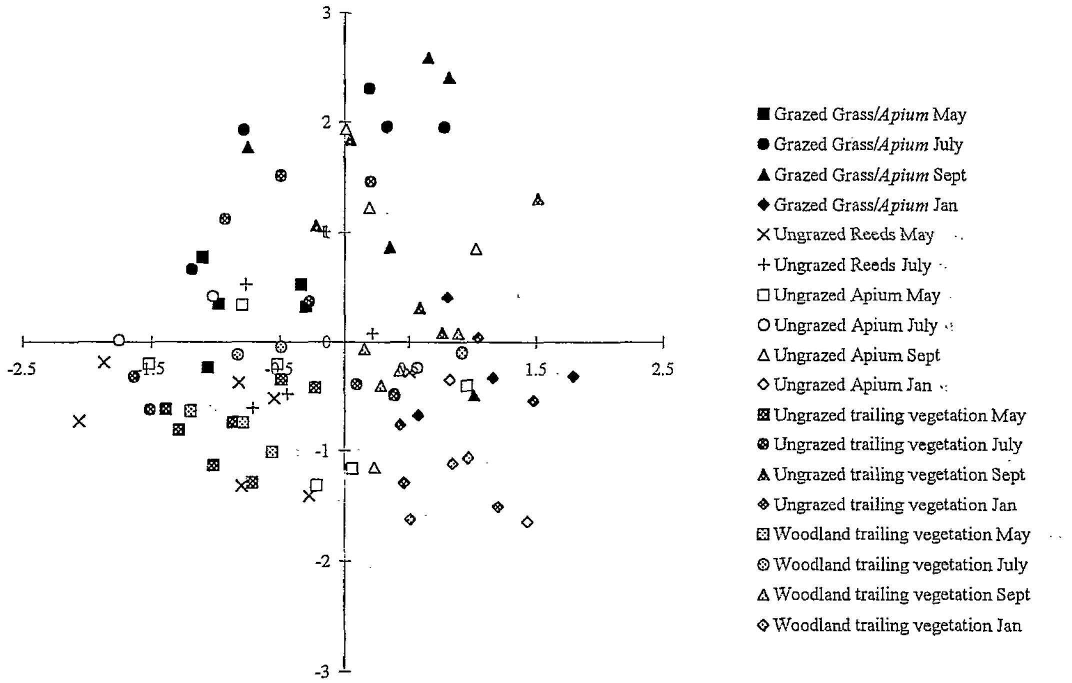
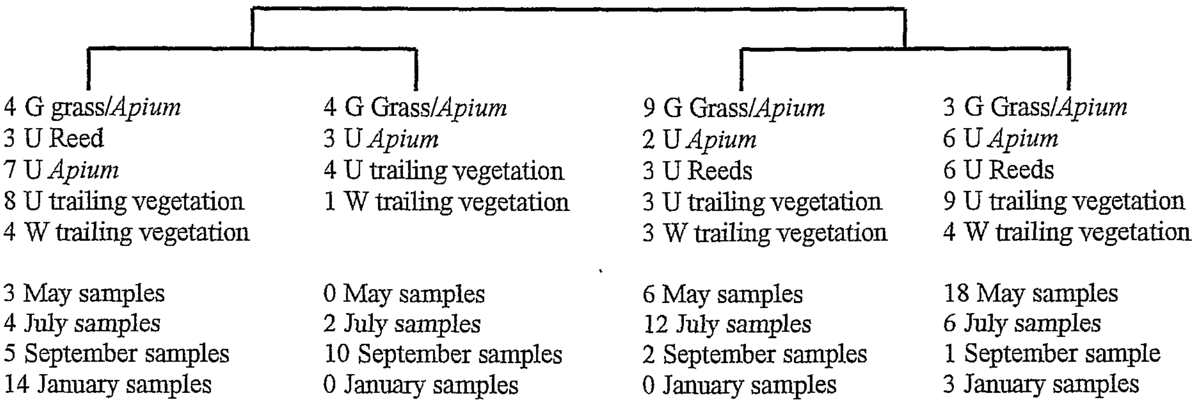


Figure 4.1. Plot of sample scores along the first two axes of a Principle Components Analysis. Samples are log-transformed abundances of invertebrate families from each marginal vegetation type (Grass/*Apium* from grazed stretches, reeds, *Apium* and trailing vegetation from ungrazed stretches and trailing vegetation from woodland stretches) taken in May, July, September and January. Replicate symbols represent different streams. There were no 'reed' samples in September or January.

Table 4.1. Eigenvalues along each of the first four ordination axes and cumulative percentage variance of data explained by each of the first four ordination axes, following a Principal Components Analysis of invertebrate communities from different types of marginal vegetation (Grass/*Apium*, Reeds, *Apium* and Overhanging vegetation) in each sampling period:

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.142	0.110	0.092	0.080
Cumulative percentage variance explained by axis	14.2	25.2	34.5	42.4

A hierarchical cluster analysis (TWINSPAN) performed on family abundance data also showed that samples from the same marginal habitat type did not cluster together (Fig. 4.2).



4 G grass/*Apium*	4 G Grass/*Apium*	9 G Grass/*Apium*	3 G Grass/*Apium*
3 U Reed	3 U *Apium*	2 U *Apium*	6 U *Apium*
7 U *Apium*	4 U trailing vegetation	3 U Reeds	6 U Reeds
8 U trailing vegetation	1 W trailing vegetation	3 U trailing vegetation	9 U trailing vegetation
4 W trailing vegetation		3 W trailing vegetation	4 W trailing vegetation
3 May samples	0 May samples	6 May samples	18 May samples
4 July samples	2 July samples	12 July samples	6 July samples
5 September samples	10 September samples	2 September samples	1 September sample
14 January samples	0 January samples	0 January samples	3 January samples

Figure 4.2. Summary of hierarchical cluster analysis of invertebrate family abundance data using TWINSPAN. Samples were taken from different types of marginal vegetation, across six streams, three management types - grazed (G), ungrazed (U) and woodland (W), and four sampling periods, May, July, September and January.

Sampling occasion, however, did show evidence of clustering. Seasonality was thus a greater factor in invertebrate community organisation than marginal habitat type.

Proportions of most abundant families

The proportions of the total invertebrate community of the 10 most abundant families from each marginal habitat, on each sampling occasion, are shown in Table 4.2 (p49). Ephemerellid and baetid mayflies, chironomids, oligochaetes, *Gammarus pulex* and *Asellus aquaticus*, hydrobiid snails and sphaeriid bivalves were numerically dominant in all habitats. Limnephilid caddis larvae were the most abundant invertebrates in January samples. There were minor differences between the different habitats. Lymnaeid and planorbid snails and corixid bugs represented a greater relative abundance in samples from grazed grass/*Apium* margins. Snails and bugs were poorly represented in woodland trailing vegetation.

Differences between margins in the abundance of individual taxa

1-way ANOVAs were performed on the abundances (log-transformed) of invertebrate and fish families across margins for each sampling occasion, in order to detect differences between different types of margin. Table 4.3 gives the summaries of the ANOVAs for families showing significant differences, together with the mean abundance of each family in each marginal habitat.

Families could be divided into two broad groups. The first group was more abundant, over one or more sampling occasions, in the Grazed grass/*Apium* margins. This included Corixidae, Veliidae, total Hemiptera, Planorbidae, Physidae, Hydracarina, Empididae, total fish (minnows and sticklebacks) and total invertebrate abundance. The other group was more abundant in trailing terrestrial vegetation, or in Ungrazed *Apium*. This group included the Elmidae, Helodidae, Simuliidae, Ceratopogonidae, total Diptera, Ephemerellidae, Leptophlebiidae, Limnephilidae, Sericostomatidae, Asellidae and Calopterygidae.

Table 4.2 . Mean relative abundance (% of total) of the 10 most abundant invertebrate families (for each habitat and month) in marginal vegetation habitats in May, July, September and January.

Family	Grazed Grass/*Apium*				Reeds	Ungrazed *Apium*				Ungrazed trailing veg.				Woodland trailing veg.			
	May	July	Sept	Jan	May	May	July	Sept	Jan	May	July	Sept	Jan	May	July	Sept	Jan
Ephemerellidae	⚫	●			●	⚫	●			⚫	●			●			
Baetidae	•	•	•		•	·	•			•	·	•		·	·	•	
Caenidae	·					·			•					·			·
Chironomidae	•	●	●	•	●	·	●	•	•	⚫	⚫	•	•	⬤	⚫	•	•
Simuliidae				·	·			●	·	•		·	•	•			
Tanypodinae									·		+						
Oligochaeta	•			·	⬤	●	•	·		·				•	•	•	•
Gammaridae	⚫	●	●	•	·	•		●	•	·	•		•	·	·	●	·
Asellidae	·	·		•	·		•		•	·	·	●	•		•	●	•
Limnephilidae	·			⬤		·			●				⬤	·	•	·	⬤
Brachycentridae					+					+							
Hydroptilidae		•			·				•	•	+		·		·	•	·
Leptoceridae													+				+
Lymnaeidae	+	•	●					·				·			·	·	
Planorbidae		·	·														
Physidae		·	●	•			•	●	•		·	•	·				
Hydrobiidae			·	•		•	·	·	●				·	•	•	•	•
Valvatidae			●														
Succineidae												•					
Sphaeriidae			·	+	·	•	•	●	·		·	·	·		·	•	·
Hydracarina	·													·			
Elmidae										·		•	·				·
Hydrophilidae							·										
Corixidae		●	•	+		·					+						
Ostracoda				·			·	·									

Key to symbols:

+	·	•	●	●	⚫	⚫	⬤
< 2%	2-5%	5-10%	10-15%	15-20%	20-25%	25-30%	> 30%

Table 4.3. Mean abundances (greatest value in bold type) of taxa showing significant differences between different marginal vegetation types, over the four sampling occasions, with results of a 1-way ANOVA performed on log-transformed abundance data.

GGA = Grazed Grass/Apium, UR = Ungrazed Reeds, UA = Ungrazed Apium, UTV = Ungrazed trailing vegetation, WTV = Woodland trailing vegetation.

Family/Order	Month	dF	F-Ratio	P	Mean abundance of taxa in each habitat				
					GGA	UR	UA	UTV	WTV
Corixidae	May	4, 17	3.362	0.033 *	**12.71**	4.32	15.42	4.97	0.11
Veliidae	May	4, 17	11.178	<0.001 ***	**11.72**	0.58	2.31	0.42	5.61
	July	3, 13	3.337	0.050 *	**17.9**	3.33	6.83	9.17	4.61
Total Hemiptera	May	4, 17	3.786	0.023 *	**22.67**	5.13	19.81	6.14	5.72
	July	3, 13	4.336	0.025 *	**164.55**	12.71	12.21	29.2	7.61
	Sept	3, 13	4.060	0.031 *	**103.23**		13.54	19.2	5.19
Planorbidae	May	4, 14	0.072	0.05 *	**7.44**	1.29	3.0	0.27	0
	Jan	3, 13	5.689	0.010 *	**16.5**		7.08	2.5	0.5
Physidae	Jan	3, 13	3.480	0.047 *	**91.93**		90.25	36.4	4.33
Hydracarina	May	4, 17	3.015	0.048 *	**23.15**	5.08	5.58	8.18	15.17
	Sept	3, 13	4.334	0.025 *	**16.9**		14.08	3.53	3.61
Empididae	Jan	3, 13	3.346	0.050 *	**8.7**		0.625	0.33	0
Total fish	May	4, 17	3.335	0.034 *	**2.06**	0.42	0.38	0.61	0.33
	July	3, 13	4.52442	0.022 *	**18.03**	0.79	2.33	3.55	0.83
	Sept	3, 12	3.48767	0.050 *	**4.9**		1.58	1.53	1.05
Total invertebrate abundance	July	3, 13	5.2364	0.014 *	**1068.2**	780.7	653.9	859.5	505.3
Elmidae	Sept	3, 13	3.553	0.044 *	8.8		26.25	**38.13**	33.61
	Jan	3, 13	3.547	0.045 *	6.83		**22.25**	18.67	12.08
Helodidae	Sept	3, 13	3.654	0.041 *	0		0	**3.67**	3.58
Simuliidae	July	3,13	4.039	0.031 *	9.1	63.65	32.5	**96.2**	15.89
	Sept	3, 13	6.682	0.006 **	15.17		**130**	18.63	1.44
Ceratopogonidae	Jan	3, 13	4.214	0.027 *	4.1		0	1.37	**10.83**
Total diptera	May	4, 17	4.182	0.015 *	96.65	127.03	37.29	**398.60**	245.83
	July	3, 13	3.867	0.035 *	160.05	338.96	160.96	**358.17**	186.72
	Sept	3, 13	6.823	0.005 **	162.23		**243.17**	124	44.44
Ephemerellidae	July	3, 13	3.669	0.041 *	112.72	68.25	**121.8**	108.4	13.83
Leptophlebiidae	Jan	3, 13	3.456	0.048 *	14.3		**13.08**	1.57	6.5
Limnephilidae	Sept	3, 13	5.080	0.015 *	0.93		0	**10.63**	9.19
Sericostomatidae	Sept	3, 13	3.890	0.035 *	0.07		0.17	4.23	**4.33**
Asellidae	Sept	3, 13	4.353	0.025 *	28.73		12.71	**140**	69.08
Calopterygidae	Jan	3, 13	3.997	0.032 *	0.7		6.0	**7.4**	0.5

4.3.2 Differences in invertebrate communities between mid-channel gravel, *Ranunculus* and marginal vegetation.

In the following analysis, samples from the different marginal habitat types, across all stretches of different management type in each of the six streams were combined to give a mean marginal vegetation sample per stream, for each sampling occasion. Similarly, gravel and *Ranunculus* samples from different stretches were combined to give mean samples of gravel and *Ranunculus* per stream. This allows comparison between marginal vegetation habitats (broadly similar to each other, from the results above) and mid-channel gravel and *Ranunculus* habitats.

Community Analysis

Following analysis of the length of the ordination axes (<2.5. s.d.), a Principal Components Analysis was performed on log-transformed family abundance data cross the three habitats (gravel, *Ranunculus* and marginal vegetation) (Ter Braak, 1987). There was little overlap between samples from the three habitats, although *Ranunculus* samples in July and September showed some similarity with other habitats (Fig. 4.3). Eigenvalues along each axis were higher than those from the PCA of samples from different marginal habitats (Table 4.4), showing stronger separation of samples from these very different habitats.

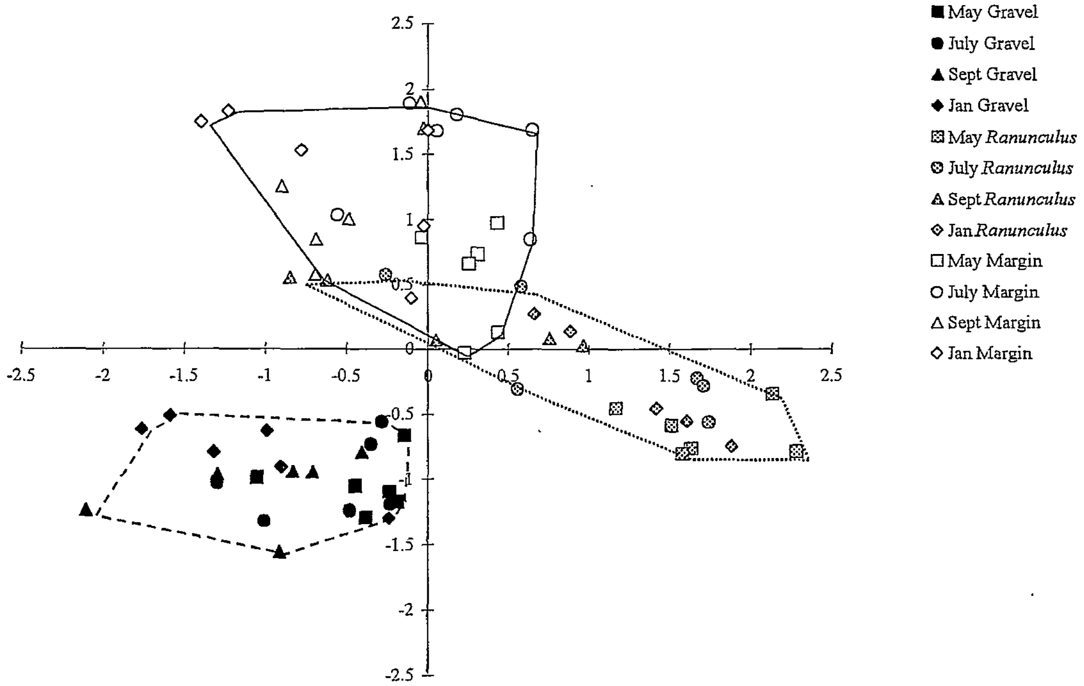
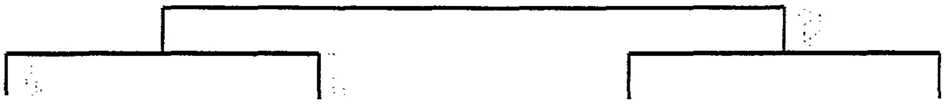


Figure 4.3. Plot of sample scores along the first two axes of a Principle Components Analysis. Samples are log-transformed abundance of invertebrate families from each habitat (mid-channel gravel, *Ranunculus*, and marginal vegetation) in May, July, September and January.

Table 4.4. Eigenvalues along each of the first four ordination axes and cumulative percentage variance of data explained by each of the first four ordination axes, following a Principal Components Analysis of invertebrate communities from the three habitats (mid-channel gravel, *Ranunculus* and marginal vegetation) in each sampling period.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.173	0.170	0.103	0.069
Cumulative percentage variance explained by axis	17.3	34.3	44.6	51.5

A hierarchical cluster analysis (TWINSPAN) performed on family abundance data showed that samples from similar habitats clustered well together (Fig. 4.4). The first division of the TWINSPAN largely separated margin samples from gravel and *Ranunculus* samples. Within the margin samples, the second division separated January samples from May and July samples, with September samples appearing on both sides of the dichotomy. On the other side of the first division, the second division largely separated *Ranunculus* from gravel samples.



0 Gravel	0 Gravel	0 Gravel	24 Gravel
0 *Ranunculus*	1 *Ranunculus*	20 *Ranunculus*	1 *Ranunculus*
16 Marginal vegetation	8 Marginal vegetation	0 Marginal vegetation	0 Marginal vegetation
6 May samples	0 May samples	6 May samples	6 May samples
6 July samples	0 July samples	6 July samples	6 July samples
4 September samples	3 September samples	3 September samples	7 September samples
0 January samples	6 January samples	5 January samples	6 January samples

Ranunculus samples also appeared in clusters of margin and gravel samples (1 each). In both cases, these were September samples.

Figure 4.4. Summary of hierarchical cluster analysis of invertebrate family abundance data using TWINSPAN. Samples were taken from patches of mid-channel gravel, *Ranunculus* and marginal vegetation, across six streams and four sampling periods, May, July, September and January.

Relative proportions of most abundant families

The proportions of the total invertebrate community of the 10 most abundant families from each habitat, on each sampling occasion, are shown in Table 4.5 (page 53). Ephemerellid and baetid mayflies, chironomids and *Gammarus pulex* were abundant in all three habitats. The habitats differed strongly in the relative abundances of other common families. Oligochaetes, caenid mayflies, elmid beetles, glossosomatid caddis (*Agapetus fuscipes*) and hydrobiid snails were relatively abundant in gravel habitats. Simuliidae were numerically dominant in *Ranunculus* samples, for most of the year. Limnephilid caddis, corixid bugs, lymnaeid and physid snails and *Asellus aquaticus* were relatively abundant in marginal vegetation.

Difference between habitats in invertebrate total abundance and taxon richness per sample.

The total abundance and taxon richness per sample was compared across the three habitats, with stream as individual replicates. 1-way ANOVAs were performed on log-transformed data on each sampling occasion, with Habitat (gravel, *Ranunculus*, marginal vegetation) as main factor. Total abundance per sample was greater in *Ranunculus* samples in May and July (Table 4.6). Taxon richness per sample, on the other hand, was lower in *Ranunculus* compared to the other two habitats in May and January and greatest in margins in July and September.

Table 4.6. Summary of 1-way ANOVAs of log-transformed total invertebrate abundance and taxon richness per sample, on each sampling occasion, with Habitat (gravel, *Ranunculus* and marginal vegetation) as main factor. * = P<0.05, ** = P<0.01, *** = P<0.001.

Invertebrate total abundance or diversity per sample	dF	F	P	*a posteriori* Tukey/Kramer pair-wise tests of significant differences between habitats
May total abundance	2, 15	9.365	0.0023**	*Ranunculus* > gravel, margins (P<0.05)
May diversity	2, 15	14.985	0.0027**	Gravel > *Ranunculus* < margins (P<0.05)
July total abundance	2, 15	8.055	0.0042**	*Ranunculus* > gravel, margins (P<0.05)
July diversity	2, 15	6.313	0.010*	Margins > Gravel (P<0.1), *Ranunculus* (P<0.05)
Sept total abundance	2, 14	0.991	0.40	
Sept diversity	2, 14	4.270	0.036*	Margins > Gravel, *Ranunculus* (P<0.1)
Jan total abundance	2, 14	0.646	0.54	
Jan diversity	2, 14	6.313	<0.001***	Gravel > *Ranunculus* < margins (P<0.05)

Rank abundance of invertebrate assemblages, equitability and diversity indices within the three habitats.

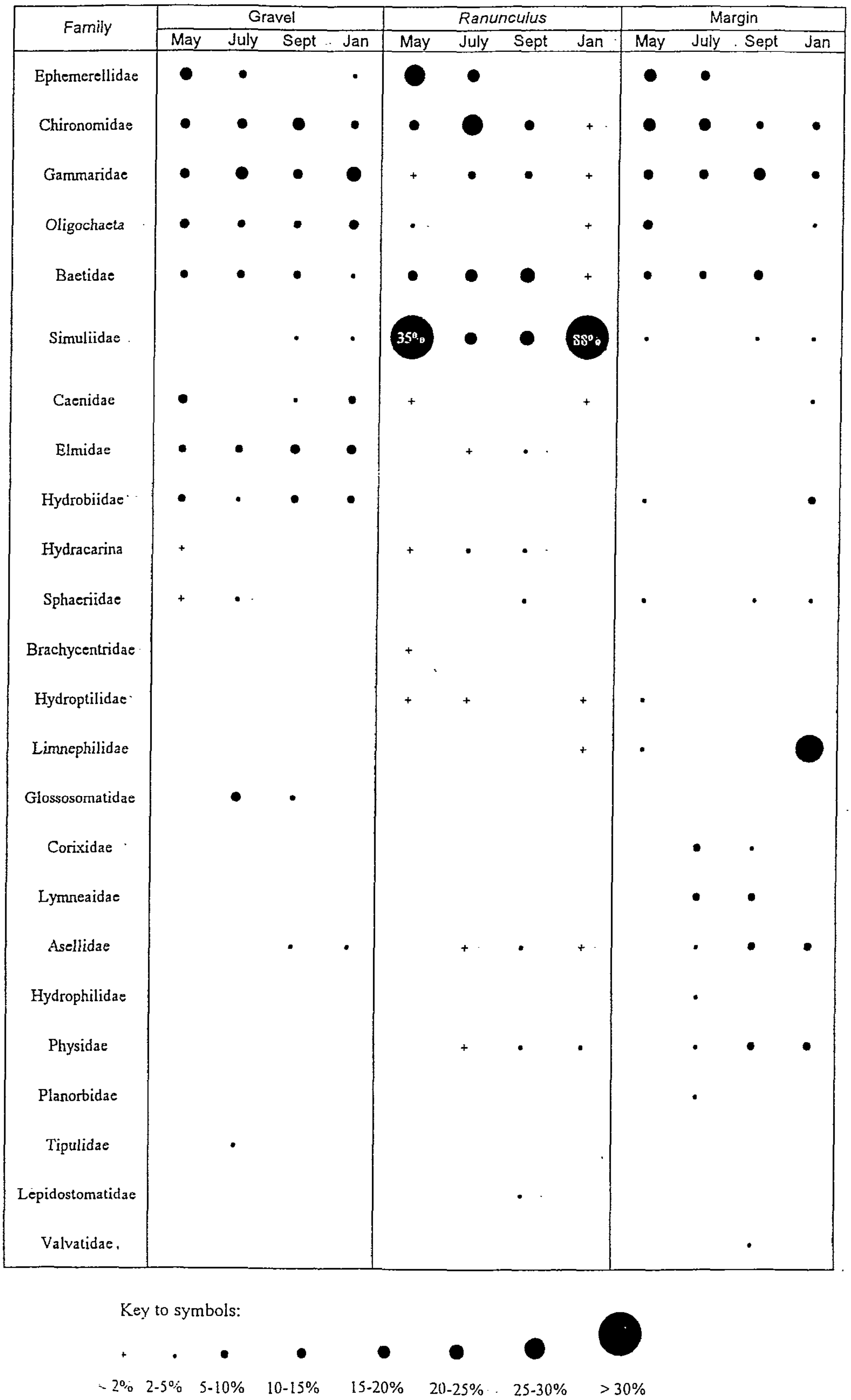
The relative proportions of the total abundance for each taxon were calculated for mean samples (of all six streams) within each habitat, on each sampling occasion. These were log-transformed and arranged in descending rank order (Fig. 4.5, page 54). Shannon diversity and equitability indices were calculated for these mean invertebrate communities from each habitat, for each sampling occasion (Table 4.7).

Table 4.7. Shannon Diversity Index (*H*) and Equitability Index (*J*) for invertebrate communities in Gravel, *Ranunculus* and Margins, based on mean samples for all streams, on each sampling occasion.

Sampling occasion	Gravel	*Ranunculus*	Marginal vegetation
May	$H = 3.983$ $J = 0.652$	$H = 2.52$ $J = 0.41$	$H = 3.987$ $J = 0.653$
July	$H = 4.169$ $J = 0.682$	$H = 3.130$ $J = 0.504$	$H = 4.597$ $J = 0.706$
Sept	$H = 4.258$ $J = 0.664$	$H = 3.537$ $J = 0.571$	$H = 4.475$ $J = 0.721$
Jan	$H = 4.350$ $J = 0.690$	$H = 1.041$ $J = 0.176$	$H = 4.715$ $J = 0.730$

Shannon diversity and equitability indices were highest for marginal vegetation on all sampling occasions, although there was little difference between marginal vegetation and gravel in May (Fig. 4.5, Table 4.7). *Ranunculus* had the lowest equitability and diversity

Table 4.5. Mean relative abundance (% of total) of the 10 most abundant invertebrate families (for each habitat and month) in the three habitats of 1) mid-channel gravel, 2) *Ranunculus* and 3) marginal vegetation in May, July, September and January.

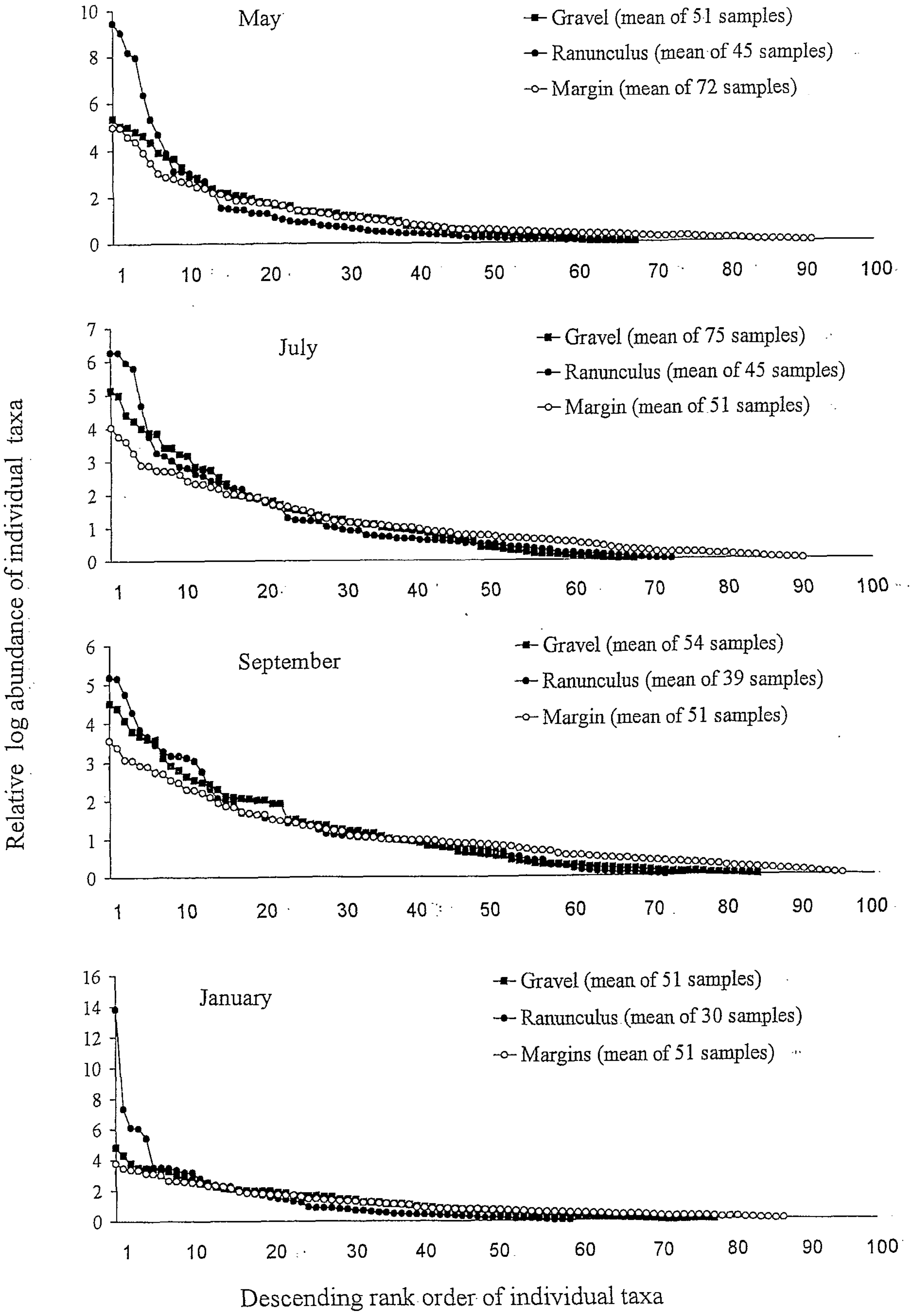


Family	Gravel				*Ranunculus*				Margin			
	May	July	Sept	Jan	May	July	Sept	Jan	May	July	Sept	Jan
Ephemerellidae	●	●		●	●	●			●	●		
Chironomidae	●	●	●	●	●	●	●	+	●	●	●	●
Gammaridae	●	●	●	●	+	●	●	+	●	●	●	●
Oligochaeta	●	●	●	●	●			+	●			●
Baetidae	●	●	●	●	●	●	●	+	●	●	●	
Simuliidae			●	●	35%	●	●	88%	●		●	●
Caenidae	●		●	●	+			+				●
Elmidae	●	●	●	●		+	●					
Hydrobiidae	●	●	●	●					●			●
Hydracarina	+				+	●	●					
Sphaeriidae	+	●					●		●		●	●
Brachycentridae					+							
Hydroptilidae					+	+		+	●			
Limnephilidae								+	●			●
Glossosomatidae		●	●									
Corixidae										●	●	
Lymneaidae										●	●	
Asellidae			●	●		+	●	+		●	●	●
Hydrophilidae										●		
Physidae						+	●	●		●	●	●
Planorbidae										●		
Tipulidae		●										
Lepidostomatidae							●					
Valvatidae											●	

Key to symbols:

+	●	●	●	●	●	●	●
< 2%	2-5%	5-10%	10-15%	15-20%	20-25%	25-30%	> 30%

Fig. 4.5. Percentage of total log abundance for individual taxa in descending rank order for all three habitats: Gravel, *Ranunculus* and Vegetated margins.



indices for all sampling occasions, indicating that this habitat was numerically dominated by only a few taxa, with relatively low diversity.

Differences in abundance of individual taxa between habitats.

A more detailed analysis of invertebrate communities was carried out on individual taxa in the three habitats. 1-way ANOVAs were performed on the mean abundance per sample of taxa with habitat (gravel, *Ranunculus*, marginal vegetation) as main factor. Replicates for the ANOVA were values from different streams. This analysis identified taxa that showed significant differences in abundance between habitats. Almost half of all taxa identified on each sampling occasion showed no significant difference in abundance between habitats, across the six streams investigated. Of 96 taxa identified in May samples, 53 showed significant differences between habitats. 56 out of 97 taxa identified in July showed significant differences, 46 out of 95 in September and 50 out of 92 in January. Tukey/Kramer pair-wise *a posteriori* tests were performed on taxa that showed significant differences, to determine where the differences lay. Table 4.8 shows the taxa which were significantly more abundant in each habitat ($P<0.05$). On each sampling occasion, more taxa were found in greater abundance in marginal vegetation, than in the other two habitats. The margins were thus an important habitat for more taxa than the other two habitats. Each habitat had a characteristic suite of invertebrates that were found in greater abundance in that habitat over the four sampling occasions (Table 4.8).

Table 4.8: Summary of habitat preferences of taxa showing significant differences ($P<0.05$) in abundance per sample between habitats, following 1-way ANOVAs performed on log-transformed data and Tukey-Kramer post-hoc pair-wise tests of significance between habitats. * denotes habitat preference and (-) denotes habitat avoidance.

Gravel	M	J	S	J
Agapetus fuscipes	*	*		*
Drusus annulatus	*	*		
Hydropsyche siltalai	*			
Hydropsyche pellucidula			*	
Odontocerum albicorne	*		*	*
Sericostoma personatum	*	*		*
Rhyacophila dorsalis		*		*
Athripsodes albifrons		*		
Athripsodes sp.		*		
Silo nigra		*		*
Elmis aenea	*	*		*
Limnius volckmari	*	*	*	*
Oreodytes sanmarkii	*	*		
Ancylus fluviatilis	*		*	*
Ephemera danica	*	*		*
Caenis rivulorum	*			
Heptagenia sulphurea			*	*
Dicranota sp.	*	*	*	*
Empididae	*			
Ceratopogonidae				*
Tabanus sp.		*	*	*
Tipula sp.				*
Tanypodinae		(-)		
Leuctra geniculata	*			
Erpobdella octoculata	*			
Glossiphonia complanata		*		
Piscicola geometra			(-)	
Gammarus pulex				*
Oligochaeta		*	*	
Physa fontinalis		(-)	(-)	
Planorbis vortex			(-)	
Mites	*			
Total (*)	15	15	8	15

Ranunculus	M	J	S	J
Ylodes conspersus	*			
Ithytrichia sp.			*	
Lepidostoma hirtum			*	
Sphaeriidae	(-)			(-)
Potamopyrgus jenkinsi	*			
Planorbis planorbis			*	
Baetis spp.	*	*	*	
Ceratopogonidae	(-)			
Ephemerella ignita	*	*	*	
Simulium sp.	*		*	*
Asellus aquaticus				(-)
Total (*)	5	2	6	1

Margins	M	J	S	J
Halesus radiatus				*
Halesus / Potamophylax sp. (small instars)				*
Limnephilus lunatus	*	*		*
Mystacides azurea	*			*
Oecetis sp.	*			*
Potamophylax cingulatus/latipennis				*
Lasiocephala basalis	*			
Agabus paludosus	*			
Agabus sp.	*			
Anacaena sp.	*	*	*	
Elodes sp.	*		*	
Helophorus brevipalpis	*	*		*
Ilybius fuliginosus	*			
Brychius elevatus		*		
Ochthebius sp.		*		
Potamonectes depressus		*		
Haliplus lineatocollis			*	
Lymnaea peregra	*	*		
Lymnaea palustris		*	*	*
Succinia sp.	*	*	*	
Planorbis vortex				*
Valvata piscinalis				*
Micronecta poweri	*	*		*
Sigara dorsalis	*	*	*	*
Sigara venusta	*		*	*
Velia caprai	*	*	*	
Corixidae (immature)		*		
Hydrometra stagnalis		*		
Nepa cinerea		*		
Stratiomyiidae	*			*
Tanypodinae	*			*
Dixa sp.	*	*	*	*
Psychodidae		*		*
Tipula sp.		*		
Limnophora sp.			*	
Chironomidae (excl. Tanypodinae)				*
Ptychopteridae				*
Baetis spp.				*
Paraleptophlebia sp.				*
Asellus aquaticus	*			
Calopteryx splendens	*		*	
Ostracoda	*			*
Crangonyx pseudogracilis		*		
Phoxinus phoxinus		*		
Gasterosteus aculeatus		*	*	
Total (*)	22	21	12	22

Habitat 'avoidance'

In addition to revealing habitats where invertebrates were more abundant than the other two habitats, the ANOVAs also showed some invertebrates were rarer in a habitat, relative to the other two (i.e. show habitat avoidance, rather than preference). Several species were significantly less abundant in gravel, compared to other habitats, including the snails *Physa fontinalis* and *Planorbis vortex,* the fish leech *Piscicola geometra* and Tanypodinae. Sphaeriidae, Ceratopogonidae and *Asellus aquaticus* were rarer in *Ranunculus* on one or more occasion. No species were significantly rarer in margins relative to other habitats.

One other method of measuring habitat avoidance is to find which species are never found in a particular habitat over all sampling occasions and across all streams. A total of 43 taxa were never found in samples from the gravel habitat, 42 taxa were never found in the *Ranunculus* habitat, yet only 8 taxa were never found in the marginal vegetation. This total (8) included five taxa that were only found in one sample throughout the entire sampling regime.

Differences in abundance of adults and egg masses between habitats

The numbers of adults and egg masses were recorded in all aquatic samples. Adults were identified to order. Egg masses were identified to order, if possible. As for aquatic invertebrates, abundances between habitats were compared using 1-way ANOVAs on mean samples from each stream, using stream as replicate. When there was a significant difference between habitats, adults and egg masses were all significantly more abundant in marginal vegetation (Table 4.9).

Table 4.9. Results of a 1-way ANOVA performed on log-transformed abundance data for adults and egg masses of invertebrates in the three habitats (Mid-channel gravel, *Ranunculus* and Vegetated Margins) on each sampling occasion. Differences between individual habitats were tested with pair-wise Tukey/Kramer *a posteriori* tests.

Month	Invertebrate Adult or Egg mass	dF	F-Ratio	P	Tukey/Kramer *a posteriori* tests > = more abundant (P<0.05) < = less abundant (P<0.05)
MAY	Trichoptera adults	2, 15	19.16	<0.01	**Margin** > Gravel, *Ranunculus*
	Trichoptera egg mass	2, 15	17.48	<0.01	**Margin** > Gravel, *Ranunculus*
	Diptera adults	2, 12	16.52	<0.01	**Margin** > Gravel, *Ranunculus*
JULY	Trichoptera adults	2, 15	13.83	<0.01	**Margin** > Gravel, *Ranunculus*
	Mollusca egg mass	2, 15	13.25	<0.01	**Margin** > Gravel, *Ranunculus*
	Coleoptera egg mass	2, 6	16.95	<0.01	**Margin** > Gravel, *Ranunculus*
	Diptera adults	2, 15	39.15	<0.01	**Margin** > Gravel, *Ranunculus*
SEPTEMBER	Mollusca egg mass	2, 15	6.34	<0.01	**Margin** > Gravel, *Ranunculus*
	Ephemeroptera adults	2, 12	23.41	<0.01	**Margin** > Gravel, *Ranunculus*
	Diptera adults	2, 15	66.78	<0.01	**Margin** > Gravel, *Ranunculus*
JANUARY	Diptera adults	2, 15	25.741	<0.01	**Margin** > Gravel, *Ranunculus*
	Unidentified egg mass	2, 12	8.506	<0.01	**Margin** > Gravel, *Ranunculus*

Relative abundance of individual taxa between habitats

To show the 'relative importance' of each habitat for the community of all individual taxa, the mean proportion of each taxon in each habitat was calculated for each sampling occasion. Firstly, the mean abundance per sample of each taxon in each of the three habitats, gravel, *Ranunculus* and margin was calculated for each stream (figures used for the ANOVAs above). Secondly, these numbers were used to calculate the proportion of each taxon in each habitat, for each stream. The results of all streams were then combined to find an overall mean proportion in each habitat for each taxon on each sampling occasion (Table 4.10, pages 61 & 62). The rank order of these proportions within each habitat was then calculated. Results are shown, in descending rank order, for each sampling occasion, in Fig. 4.6 (page 60). It can be seen that margins have an overall greater proportion of individual taxa than either gravel or *Ranunculus*; and gravel has a greater overall proportion of taxa than *Ranunculus*, for all sampling occasions.

The mean proportion per taxon in each habitat was calculated for each sampling occasion (Fig. 4.7). This is simply the sum of all proportions within each habitat, divided by the number of taxa. This reflects the average abundance per taxon in each of the three habitats. If many taxa were rare in a particular habitat, relative to other habitats, then the mean relative abundance per taxon will be low. If however, many were common in one particular habitat, relative to others, then the mean relative abundance per taxon will be high.

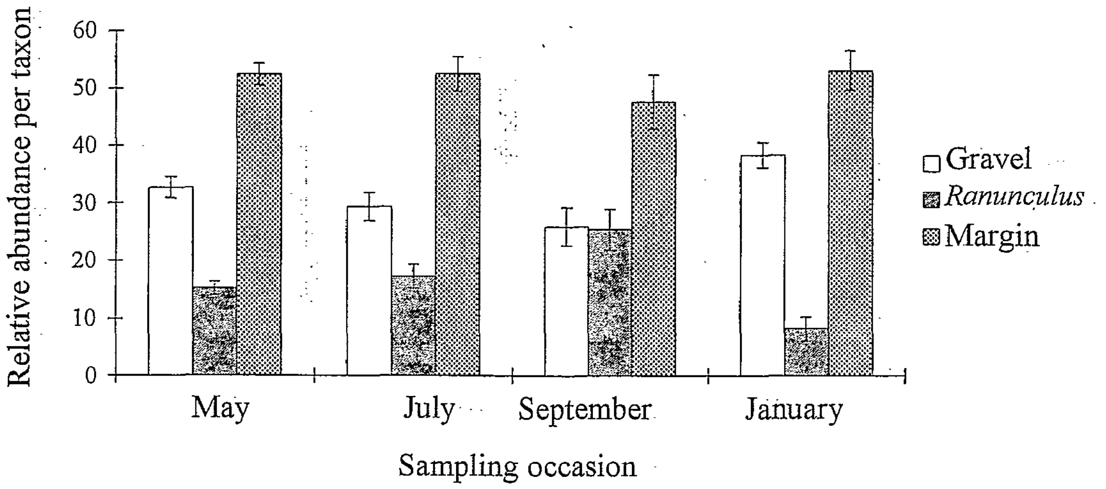


Figure 4.7. Mean relative abundance per taxon in the three habitats (mid-channel gravel, *Ranunculus* and vegetated margins) for all sampling occasions. Mean (six streams) +1S.E.

On all sampling occasions, there was a significantly greater mean proportion per taxon in the margins (Fig. 4.7, Table 4.11 – pg65). Margins were thus relatively more important for the total assemblage of invertebrates. The relative abundance per taxon in *Ranunculus* was lowest, but showed a rise to a maximum in September, reflecting an increasing relative importance of *Ranunculus* as a habitat over the summer.

Fig. 4.6. Descending rank order of mean proportions of individual taxa within the three habitats, for each habitat (Main channel gravel, *Ranunculus*, Marginal Vegetation). May, July, September 1996 and January 1997.

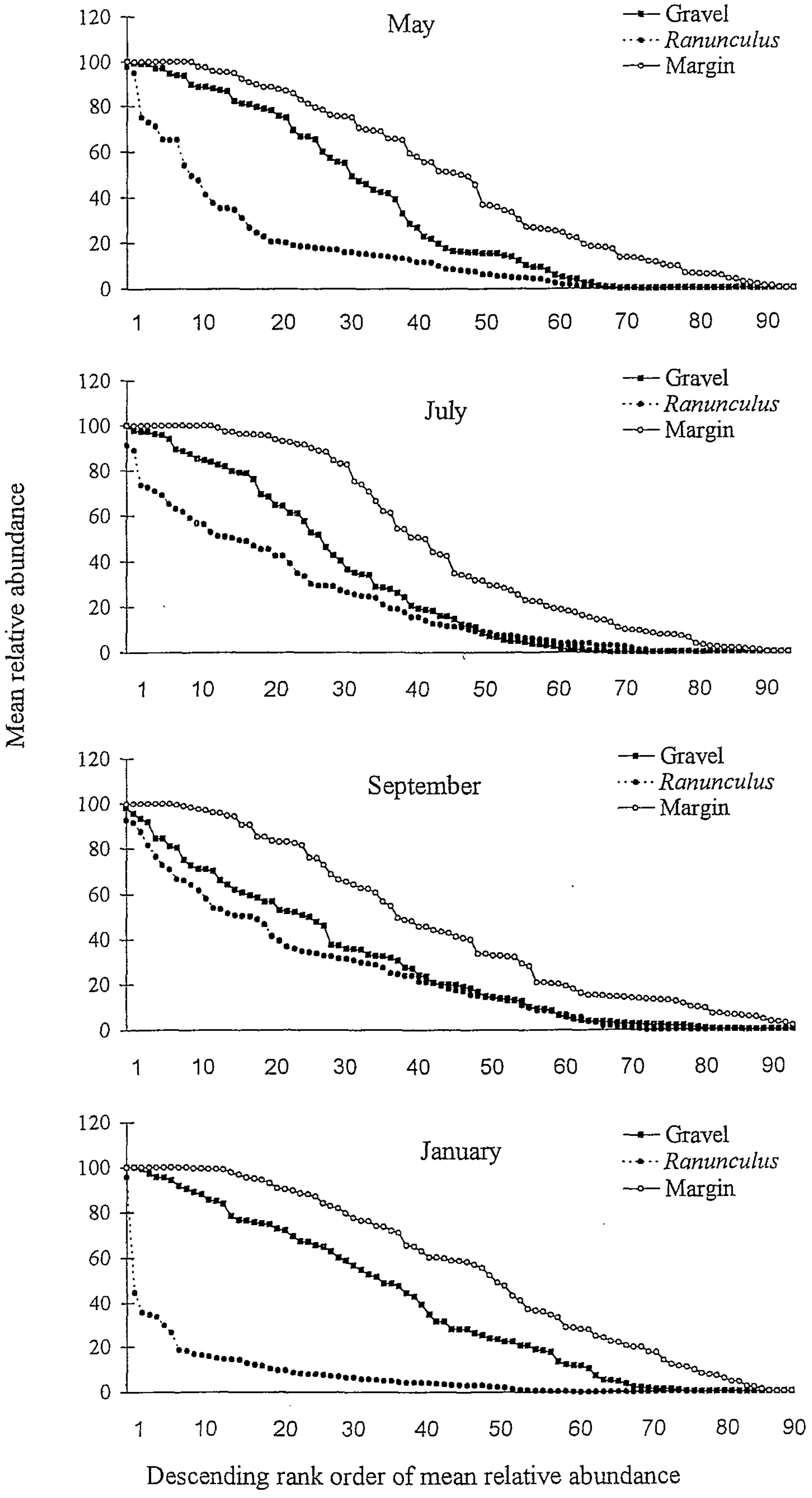


Table 4.10: Mean percentage of taxa in each habitat, for each sampling occasion.
G = Gravel, R = *Ranunculus*, M = Marginal vegetation

	May			July			Sept			Jan		
	G	R	M	G	R	M	G	R	M	G	R	M
Agapetus fuscipes	87.00	0.00	13.00	96.20	3.10	0.80	95.50	1.30	3.30	100.00	0.00	0.00
Anabolia nervosa				82.50	0.00	17.50				0.00	0.00	100.00
Athripsodes albifrons	78.90	11.50	9.50	87.40	11.10	1.60						
Athripsodes cinerea	54.80	11.60	33.60									
Athripsodes sp.	81.00	13.10	5.90	69.50	27.20	3.30				56.50	14.70	28.80
Brachycentrus subnubilis	9.50	65.30	25.20	28.40	69.20	2.40	2.20	81.50	16.30	51.60	34.60	13.80
Drusus annulatus	96.90	3.10	0.00	100.00	0.00	0.00				91.80	8.20	0.00
Goera pilosa							35.60	50.20	14.20			
Halesus radiatus	69.10	17.90	13.00	12.00	14.10	73.90				0.10	9.70	90.20
Halesus/Potamophylax (small instars)				7.20	4.00	88.70				0.50	8.80	90.70
Hydropsyche pellucidula				34.00	56.20	9.80	60.70	33.70	5.60	85.50	6.50	7.90
Hydropsyche siltalai	89.60	8.80	1.60	51.60	46.80	1.60	56.70	29.80	13.50	76.70	5.70	17.60
Hydropsyche sp.	22.90	65.50	11.60									
Hydroptila sp.	16.10	35.20	48.70	26.00	48.70	25.30	47.50	31.40	21.10	88.00	0.00	12.00
Ithytrichia sp.	14.30	34.50	51.20	0.00	70.80	29.20	1.00	92.80	6.30	13.30	26.40	60.30
Lasiocephala basalis	0.00	0.00	100.00				0.00	0.00	100.00	2.20	15.80	81.90
Lepidostoma hirtum	21.90	22.90	55.30	34.30	45.30	20.40	3.00	91.60	5.40	47.30	16.30	36.40
Limnephilus lunatus	0.00	12.50	87.50	0.50	9.40	90.10				0.10	3.20	96.60
Mystacides azurea	0.00	0.00	100.00	5.00	91.20	3.80	19.70	19.50	60.80	3.50	7.90	88.60
Oecetis sp.	4.10	20.60	75.30				0.00	0.00	100.00	0.00	12.00	88.00
Odontocerum albicorne	100.00	0.00	0.00	84.50	6.40	9.00	81.00	14.60	4.40	90.40	0.00	9.60
Polycentropus flavomaculatus	86.60	0.00	13.40				23.60	61.80	14.60	18.50	18.50	63.10
Polycentropus sp.	0.00	0.00	100.00									
Potamophylax cingulatus/latipennis	38.80	15.80	45.40	8.30	0.00	91.70	16.90	0.00	83.10	28.10	11.50	60.30
Rhyacophila dorsalis	57.10	37.40	5.50	52.70	39.00	8.40	37.20	50.00	12.80	83.70	14.40	1.90
Sericostoma personatum	88.60	0.00	11.40	97.30	1.00	1.70	49.80	6.60	43.50	76.40	3.30	20.30
Silo nigricornis				78.90	21.10	0.00	64.20	29.30	6.50	99.10	0.60	0.30
Ylodes conspersus	2.50	75.00	22.50									
Unid. Limnephilidae							18.40	0.00	81.60			
Agabus palludosus	0.00	0.00	100.00	0.00	0.00	100.00						
Agabus spp.	0.00	0.00	100.00	1.60	10.20	88.20	56.80	10.90	32.20			
Anacaena sp.	4.90	0.00	95.10	0.00	6.20	93.80	0.00	0.00	100.00			
Brychius elevatus				85.30	7.00	7.70	70.90	9.80	19.30	52.70	4.30	43.00
Elmis aenea	66.30	15.90	17.80	57.60	29.30	13.10	52.90	32.70	14.30	75.60	4.50	19.90
Elodes sp.	6.00	5.60	88.40	0.00	0.00	100.00	0.00	5.70	94.30	34.80	6.50	58.70
Gyrinus urinator	42.20	0.00	57.80	0.00	29.30	70.70	84.60	0.00	15.40	26.30	0.00	73.70
Haliplus lineaticollis							4.00	0.00	96.00			
Haliplus sp.							14.70	0.00	85.30			
Helophorus brevipalpis	0.00	2.50	97.50	0.40	2.50	97.10				23.80	0.00	76.20
Helophorus grandis	0.00	0.00	100.00									
Helophorus sp.	0.00	72.90	27.10							0.00	0.00	100.00
Ilybius uliginosus	0.00	0.00	100.00				3.80	1.70	94.50			
Limnius volckmari	97.00	0.80	2.20	95.70	3.10	1.20	93.10	3.30	3.50	95.30	0.30	4.30
Ochthebius sp.	0.00	97.50	2.50	0.00	0.00	100.00						
Oreodytes sanmarkii	99.10	0.00	0.90	79.10	5.60	15.40	75.10	18.00	6.90	28.00	0.00	72.00
Platambus maculatus				0.00	0.00	100.00	14.00	17.40	68.60	0.00	0.00	100.00
Potamonectes depressus	0.00	35.10	64.90	5.50	19.30	75.20	5.80	28.80	65.50			
Orectochilus villosus				1.20	15.60	83.20	31.70	27.60	40.70	17.60	17.00	65.40
Oulimnius dilatus	75.70	4.90	19.40							69.40	5.70	24.90
Ancylus fluviatilis	79.50	14.40	6.10	64.20	26.20	9.60	70.20	20.50	9.30	85.00	7.60	7.40
Bithynia tentaculata	15.80	13.90	70.30	18.80	19.20	62.00	2.40	24.60	73.00	20.50	0.00	79.50
Lymnaea palustris	0.00	13.30	86.70	1.50	2.70	95.70	2.30	31.20	66.60	4.50	1.00	94.50
Lymnaea peregra	12.20	18.90	68.80	3.70	11.70	84.70	2.70	14.20	83.10	31.50	12.80	55.60
Lymnaea stagnalis	0.00	4.20	95.80	0.00	17.50	82.50	1.70	15.70	82.60			
Sphaeridae	43.00	1.80	55.20	46.00	24.50	29.50	8.30	50.60	41.10	28.10	6.90	65.00
Physa fontinalis	15.80	18.70	65.50	3.40	42.30	54.30	1.70	49.00	49.40	11.80	35.80	52.40
Planorbis planorbis	4.00	20.00	76.00	4.90	45.30	49.70	0.00	66.30	33.70	0.90	0.00	99.10
Planorbis vortex	15.30	15.00	69.70	1.70	5.30	93.00	3.50	13.00	83.50	11.70	4.20	84.10
Planorbis sp.				0.00	8.60	91.40	3.70	39.40	56.90	22.30	0.00	77.70
Potamopyrgus jenkinsi	65.30	0.60	34.10	64.70	12.30	23.10	71.10	8.60	20.30	39.10	1.20	59.70
Succinea sp.	0.00	14.50	85.50	0 00	0.00	100.00	0.00	0.00	100.00	0.00	0.00	100.00
Theodoxus fluviatilis				24.20	42.40	33.40						
Valvata cristata										10.40	0.00	89.60
Valvata piscinalis	16.30	5.30	78.30	3.00	0.00	97.00	2.80	6.70	90.50	0.90	0.00	99.10

Table 4.10 (cont'd.).

	May			July			Sept			Jan		
	G	R	M	G	R	M	G	R	M	G	R	M
Corixidae sp.				0.10	1.00	98.90	35.50	0.00	64.50			
Gerris lacustris	0.00	0.00	100.00	0.00	0.00	100.00						
Hydrometra stagnalis	2.40	0.00	97.60	0.00	0.00	100.00	1.90	0.00	98.10	0.00	0.00	100.00
Micronecta poweri	0.00	0.00	100.00	0.00	3.90	96.10				0.00	0.00	100.00
Nepa cinerea				0.00	0.00	100.00	0.00	0.00	100.00			
Sigara dorsalis	0.00	17.10	82.90	0.00	7.50	92.50	1.50	1.60	96.90	0.20	0.20	99.50
Sigara venusta	0.00	0.00	100.00	0.00	0.00	100.00	0.00	0.50	99.50	0.00	0.70	99.30
Sigara sp.							2.60	0.00	97.40			
Velia caprai	0.00	7.90	92.10	0.00	0.00	100.00	0.00	0.00	100.00			
Baetis spp.	15.30	71.30	13.40	11.80	73.80	14.50	9.10	72.80	18.10	44.30	44.70	10.90
Caenis luctuosa	66.40	7.30	26.30	28.80	61.70	9.60	20.00	34.30	45.70	20.70	5.60	73.80
Caenis rivulorum	87.80	6.10	6.10	68.50	24.10	7.40	72.80	17.00	10.20	72.50	3.50	24.00
Caenis sp.							59.50	30.70	9.90	75.10	5.00	19.90
Ecdyonurus dispar				89.20	0.00	10.80						
Ephemera danica	88.50	1.40	10.10	97.70	0.00	2.30	52.20	32.40	15.40	95.60	0.30	4.10
Ephemerella ignita	17.60	65.30	17.10	14.70	62.90	22.40	14.80	64.30	21.00	48.50	29.70	21.80
Heptagenia sulphurea	55.30	26.70	18.00	61.00	24.90	14.10	84.40	8.70	6.80	78.40	14.60	7.00
Paraleptophlebia sp.	0.00	24.40	75.60				10.20	76.70	13.00	12.20	4.90	82.90
Ceratopogonidae	74.80	0.70	24.50	60.90	7.50	31.60	80.40	8.10	11.50	62.80	4.00	33.20
Chironomidae	19.50	53.90	26.70	18.40	59.00	22.60	33.30	53.20	13.50	31.40	10.40	58.20
Dicranota sp.	98.90	0.90	0.20	94.00	4.70	1.30	91.70	5.60	2.70	97.10	1.90	1.00
Dixa sp.	0.00	4.70	95.30	2.50	1.70	95.90	0.10	1.00	98.90	0.00	0.00	100.00
Empididae	82.20	8.40	9.50	36.20	29.10	34.70	30.40	41.40	28.20	23.20	0.40	76.30
Limnephila sp.	48.80	0.00	51.20							58.80	0.00	41.20
Limnophora sp.	9.30	0.00	90.70	0.00	72.70	27.30	12.80	1.80	85.40	67.00	4.20	28.70
Psychodidae	45.60	4.70	49.70	0.70	4.00	95.40	9.40	0.00	90.60	5.00	0.00	95.00
Ptychopteridae							0.00	0.00	100.00	0.00	0.00	100.00
Simulium sp.	1.00	95.10	4.00	4.80	88.90	6.30	6.50	87.50	6.00	2.10	95.70	2.20
Stratiomyiidae	0.50	18.40	81.10	0.00	0.00	100.00	24.10	0.00	75.90	7.10	0.00	92.90
Tabanus sp.				97.10	2.90	0.00	98.30	0.00	1.70	100.00	0.00	0.00
Tanypodinae	7.90	17.20	74.90	6.70	50.90	42.40	20.00	35.90	44.10	1.60	2.90	95.50
Tipula sp.	93.50	0.00	6.50	0.00	0.00	100.00	50.70	3.70	45.60	94.30	0.00	5.70
Asellus aquaticus	28.30	6.10	65.60	19.40	30.10	50.60	13.20	53.70	33.00	25.40	3.80	70.80
Crangonyx pseudogracilis	15.40	15.40	69.20	34.80	3.90	61.30				43.00	0.00	57.00
Gammarus pulex	46.80	17.50	35.60	42.70	25.50	31.90	32.70	34.80	32.50	64.60	7.30	28.10
Ostracoda	10.30	0.00	89.70	11.20	34.60	54.20	4.30	0.00	95.70	5.10	8.00	86.90
Calopteryx splendens	0.60	4.60	94.80	0.00	33.50	66.50	0.50	36.80	62.70	0.00	2.20	97.80
C. virgo							13.90	70.90	15.20			
Erpobdella octoculata	80.70	1.00	18.30	20.50	51.10	28.40	26.90	25.00	48.10	72.00	0.30	27.70
Glossiphonia complanata	59.80	9.90	30.40	83.90	9.20	6.90	45.80	14.30	39.90	67.30	15.20	17.50
Helobdella stagnalis	78.00	0.00	22.00	27.80	52.80	19.30	27.50	58.00	14.50	88.90	0.00	11.10
Pisicola geometra	0.00	41.10	58.90	0.00	56.90	43.10	4.90	46.50	48.60	22.20	19.00	58.90
Theromyzon tessulatum							58.40	21.10	20.50			
Leuctra fusca	94.40	1.90	3.70	79.60	12.70	7.80	52.00	15.10	32.90			
Leuctra geniculata	99.00	0.00	1.00	88.60	11.40	0.00						
Isoperla grammatica										59.90	3.00	37.10
Hydracarina	26.80	47.40	25.70	15.90	65.30	18.80	20.80	66.70	12.50	54.60	9.60	35.90
Tricladia	41.80	7.60	50.60	40.20	15.60	44.20	35.70	21.40	42.90	48.60	2.40	49.00
Oligochaeta	32.80	30.90	36.30	76.10	7.60	16.30	62.00	24.10	13.90	74.70	2.90	22.40
Lumbricidae	93.70	0.00	6.30	81.80	0.00	18.20	66.20	0.00	33.80	65.50	0.00	34.50
Sialis fuliginosus				0.00	49.40	50.60	37.50	0.00	62.50			
Gasterosteus aculeatus	0.00	20.70	79.30	0.00	0.00	100.00	0.00	24.00	76.00	0.00	0.00	100.00
Cottus gobio	14.00	49.30	36.70	16.10	50.10	33.90	19.10	51.40	29.40	18.70	33.70	47.50
Phoxinus phoxinus	0.00	11.40	88.60	0.00	3.90	96.10	32.40	12.90	54.70	1.00	0.00	99.00

Table 4.11. Results of a 1-way ANOVA performed on mean relative abundance per taxon (arcsine-transformed) in each of the three habitats, mid-channel, *Ranunculus* and vegetated margins over the four sampling occasions. Individual streams (n =5 or 6) are replicates. *** = P<0.001, ** = P<0.01

Sampling occasion	dF	F-Ratio	P
May	2, 15	117.733	<0.001 ***
July	2, 15	48.685	<0.001 ***
September	2, 12	10.961	0.002 **
January	2, 12	66.383	<0.001 ***

The presence of 'rare' taxa in each habitat

Rare taxa in this study were arbitrarily defined as those taxa found in less than 5% of all samples. Taxa that were solely found in one habitat are shown in Table 4.12. Many more such taxa were found in marginal vegetation than in the other two habitats.

Table 4.12. Rare taxa found solely in one habitat only across the six streams and four sampling occasions. (Total number of taxa found in all samples = 159. Number of taxa found in < 5% of samples = 49).

Mid-channel gravel	***Ranunculus***	**Margins**
Hydatophylax infumatus	*Psychomyia pusilla*	*Beraeodes minutus*
Rhithrogena semicolorata	*Dryops* sp.	*Limnephilus politus*
Cordulegaster boltonii	*Leuctra hippopus*	*Lype reducta*
Atherix sp.		*Oxyethira* sp.
		Agabus didymus
		Dytiscidae sp.
		Haliplus obliquus
		Helophorus grandis
		Hydrobius fuscipes
		Hydroporus tesselatus
		Laccobius bipunctatus
		Laccophilus hyalinus
		Laccophilus minutus
		Ochthebius pusillus
		Brachycercus harrisella
		Curculionidae
		Ephydridae
		Sciomyzidae
		Hesperocorixa sahlbergi
		Notonecta glauca
		Plea leachi
		Corixidae indet.
		Coenagrion puella
		Austropotamobius pallipes
Total = 4	**Total = 3**	**Total = 24**

4.4 Discussion

4.4.1 Differences in invertebrate communities between types of marginal vegetation

The ordination and cluster analysis of invertebrate communities showed that there was little overall difference between communities from the different types of marginal vegetation, although individual families were more abundant in certain kinds of margin. Seasonal differences (governed by changes in macrophyte architecture, and invertebrate life histories, for example) were apparently much greater than differences between individual marginal vegetation types.

Bugs, some snails and small fish (minnows and sticklebacks) were more abundant, in spring and summer, in the grassy margins of stream sections running through grazed meadows. These margins were characterised by the abundance of small shallow 'pondlets', which were created by the poaching action of cattle grazing or drinking at the water's edge. Bugs and snails may have favoured low current velocities and high periphyton density or plant debris on the silty substrate in these margins. They may also have favoured locally high temperatures in the silty pondlets in spring and summer. Minnows have been shown to use shallow marginal habitats of chalk streams for energetic reasons, where the warmer temperatures in shallow, silty margins allow greater growth of fish (Garner *et al.*, 1998). The other groups of invertebrates that were less common in grassy margins may have preferred habitats with greater current velocities, or greater physical habitat structure. Adult oviposition may also have been less in grassy margins, where there was little terrestrial bank vegetation structure to facilitate adult reproduction.

In flowing waters, the relationship between macrophytes and invertebrates tends to be dominated by abiotic factors, such as flow and substrate conditions within the macrophyte stands. The abundance of certain invertebrate groups in macrophyte stands in the mid-channel flow has been found to be related to the degree to which the macrophytes influence local flow and substrate conditions (Harrod, 1964; Vincent *et al.*, 1982; Dudley, 1983; Wright *et al.*, 1983; Rooke, 1984; Gregg & Rose, 1985). However, little relationship has been found between invertebrate communities and stands of different species of marginal macrophyte in flowing waters (Vincent *et al.*, 1982; Wright *et al.*, 1994; Armitage *et al.*, 1995; Pardo & Armitage, 1997), suggesting that physical conditions in different types of stream marginal vegetation are broadly similar, with respect to flow, substrate and structural complexity. The scale of investigation will undoubtedly have an important influence on whether discreet invertebrate assemblages are found in different marginal vegetation types. Large-scale sweep sampling (over several metres) of a macrophyte stand may include other habitats, despite efforts to sample single-species stands. Fine-scale sampling techniques, for example, harvesting individual stems of macrophytes with their associated macrophytes, may be more accurate at identifying specific macrophyte-invertebrate associations.

In marginal vegetation in still waters, such as lake littorals, macrophytes with different surface area characteristics, stand density or growth forms have been found to have different invertebrate communities (Dvorak & Best, 1982; Scheffer *et al.*, 1984; Cyr & Downing, 1988; Brown *et al.*, 1988; Chilton, 1990; Olson *et al.*, 1995). This indicates that, in the absence of interaction with flow, other factors associated with different macrophyte species, such as amount of substrate available for colonisation, growth form in the water column and protection from predators become important for invertebrate communities.

A significant finding in this study is the relative importance of terrestrial vegetation trailing in the water at stream margins. This habitat had as abundant and diverse an invertebrate community as semi-emergent marginal macrophytes, such as stands of *Apium* or reeds. In woodland sections, the invertebrate community in the sparse marginal vegetation (consisting of occasional trailing stems and leaves of terrestrial plants, such as ivy and water-dropwort) was almost as abundant and diverse as that in much more abundant marginal emergent vegetation in open sections. Despite confirmation of the importance of vegetation that provides a physical transition between water and land (Ward *et al.*, 1998), this kind of marginal habitat is virtually ignored in stream invertebrate studies. Management of the terrestrial banks will greatly influence the degree and potential of trailing vegetation in the water. In streams with little marginal semi-emergent vegetation (for example, due to high erosive force on the banks), trailing terrestrial vegetation may be the only 'soft' (sensu Rutt *et al.* 1989), structurally complex vegetated habitat in the stream. In addition, trailing vegetation was found to persist in this study over winter, even when the plants themselves were dead or senescent. Such a habitat is thus likely to be even more important during late winter when emergent in-stream macrophytes die back.

Discovery of the importance of trailing vegetation is likely to have important implications for current riparian management. Removal of dead bankside plants that have fallen into stream channels is usually undertaken to expedite the flow of winter floodwaters. Autumn cutting of bankside and marginal vegetation is thus often endorsed as a 'least damaging' option. However, where flood risk is minimal, or in areas where flooding is sanctioned, non-clearance of such vegetation would be of significant benefit over-wintering invertebrate communities, with presumable economic savings for riparian managers.

4.4.2 Differences between channel gravel, *Ranunculus* and marginal vegetation

There were strong differences between invertebrate communities in marginal vegetation habitats compared to mid-channel gravel and *Ranunculus* habitats. Both ordination and cluster analysis showed that invertebrate communities from the three habitats were consistently distinct from each other, over all four sampling occasions. The slight overlap between marginal macrophytes and *Ranunculus* invertebrate communities in July and particularly September indicated that physical conditions in the two habitats resembled each other somewhat. In the summer, during conditions of low flow and high macrophyte abundance, some marginal macrophyte and *Ranunculus* stands tended to merge together at the edges of the channel. Flow rates in such *Ranunculus* habitats were typically low, such that they approached those typical of marginal vegetation. During periods of higher flow and lower macrophyte abundance, the two habitats were physically separated and had very different flow regimes.

Overall, each habitat was characterised by a distinctive 'suites' of invertebrates, although many numerically dominant groups or taxa, such as chironomids, *Gammarus pulex* and mayfly nymphs were abundant in all three habitats. The gravel habitat contained a characteristic group of invertebrates that included cased and case-less caddis and mayflies associated with stony substrata, the elmid riffle beetles and gravel-dwelling Dipteran larvae. Other taxa were associated with gravel on only one sampling occasion, reflecting either temporal habitat shifts, or only weak associations with the mid-channel gravel, such as that exhibited by *Gammarus pulex*. *Ranunculus* had a very distinct group of invertebrates, principally the mayfly nymphs *Baetis* spp. and *Ephemerella ignita* and the blackfly larva *Simulium* spp. Two caddis larvae were also characteristic of this habitat – *Ylodes conspersa* and *Ithytrichia* sp. The caddis *Brachycentrus subnubilus* that is very common in *Ranunculus* beds in lower stretches of chalk streams (Gunn, 1984) was less common in this study of small chalk streams. Interestingly, *Ranunculus* beds are listed as a natural habitat type with special Conservation status under Annex 1 of the Habitats Directive (92/43/EEC). Marginal vegetation however had a larger group of characteristic invertebrates than either gravel or *Ranunculus*. There were particularly high numbers of snails (excluding the small hydrobiid snail *Potamopyrgus jenkinsi*), true bugs, large beetles, fly larvae, small fish and damselfly nymphs.

Many other studies have found the lotic invertebrate community in macrophytes to differ from those in other, mineral habitats, particularly in terms of diversity and abundance (Wright *et al.*, 1983; Jenkins *et al.* 1984; Ormerod *et al.*, 1987; Ormerod, 1988; Rutt *et al.*, 1989; Minshall 1984; Anderson & Day, 1986; Gregg & Rose, 1985; Suren 1991; Palmer *et al.*, 1991; Wright *et al.*, 1992; Harper *et al.*, 1992; Wright *et al.*, 1994; Armitage *et al.*, 1995; Cogerino *et al.*, 1995). These differences, in flowing waters, are usually ascribed to abiotic factors associated with macrophyte beds, including increased surface area (Gregg & Rose, 1985; Dudley, 1988), flow reduction (Vincent *et al.*, 1982; Gregg & Rose, 1985; Wright *et al.*, 1992) sediment characteristics (Vincent *et al.*, 1982) and detritus and periphyton accumulation (Brown *et al.*, 1988; Wright *et al.*, 1992; Wright *et al.*, 1994). Differences in the invertebrate communities between *Ranunculus* and marginal vegetation in this study were very marked and probably mainly reflected physical differences in flow conditions and structural complexity. For much of the year, *Ranunculus* beds were dominated by *Simulium* larvae and mayfly larvae, which occur in greatest abundance in areas of high flow (Fitter & Manuel, 1986).

Differences between habitats have also been ascribed to biotic factors, including predator-avoidance by vulnerable taxa (Ormerod, 1988; Brown *et al.*, 1988). Fish in particular are unlikely to be able to hunt efficiently in structurally complex and shallow margins, as has been found in marginal vegetation in lake littorals (Crowder & Cooper, 1982; Gilinsky, 1984; Bronmark, 1988; Lauridsen & Lodge, 1996; Eklov, 1997). Many invertebrate species may also live in the margins simply because adults laid their eggs there (Harrod, 1964; Soska, 1975; Suren, 1991). The high numbers of small instar limnephilid caddis in the margins in January probably reflected oviposition in the margins by winged adults, rather than intrinsic choice for this habitat by the larvae, which occurred abundantly in gravel as later instars. The marginal vegetation itself will provide both food, directly for those species that can consume live and decaying plant material, (Jacobsen & Sand-Jensen, 1992; Newman *et al.* 1996) and indirectly, through the high abundance of periphyton on leaves and stems of plants.

A key factor of marginal vegetation is the variability of the habitat. Not only is the habitat structurally complex, but margins possess elements of the other two mid-channel habitats. Where marginal vegetation is entrained in high flows at the interface between margins and flowing water, the habitat will resemble that of the trailing stems and leaves of mid-channel *Ranunculus*. For taxa that live on the surface of stones and gravel, rather than burrowing between or underneath them, the large, relatively fixed stems of marginal vegetation may provide a similar physical habitat and may also have similar resource levels, such as periphytic algae.

The variability of a habitat will have a large influence on the faunal community in that habitat (Thienemann, 1950). The first two of Thienemann's basic principles (Thienemann, 1950; quoted in Macan, 1977) state that:

1. The more variable the conditions in a biotope, the greater are the number of species inhabiting it.

2. The more conditions in a biotope depart from the normal and from the optimum for most organisms, the poorer it will be in species, the more characteristic will the community be, and the greater will be the number of those species that do occur.

The higher invertebrate diversity of marginal vegetation (in July and September), indicated this habitat was more variable than the other two mid-channel habitats. The lower diversity and equitability indices of gravel and particularly *Ranunculus* also indicated that these latter habitats were more uniform and were dominated by only a few species. *Ranunculus* was numerically dominated by mayflies and *Simulium* larvae and had the greatest total invertebrate abundance per sample (in May and July). Many taxa avoided gravel and *Ranunculus* altogether, over the course of the investigation, whereas only very few taxa were never found in margins (which in this respect acted as 'generalist reservoirs'). *Ranunculus* and, to a lesser extent the mid-channel gravel, can thus be thought of as relatively extreme habitats, poor in taxa and dominated by a few characteristic taxa. The suitability of marginal vegetation for many taxa can also be seen in the rank distribution of proportions of taxa in each habitat and the mean proportion per taxon in each habitat. Although margins possess many 'specialists' such as the true bugs and many beetles and snails, many other taxa were present in high proportions in the margins, even if they were more abundant in other habitats. The margins were thus strongly favoured by a few taxa, suitable for many taxa and only disfavoured by a few taxa. *Ranunculus*, on the other hand, was strongly favoured by only a very few taxa, suitable for only a few and strongly disfavoured by many. Gravel was intermediate between the two. Margins can thus be thought of as the most critical habitat for the whole invertebrate community in a small chalk stream ecosystem, although the high invertebrate abundance per sample in *Ranunculus* beds demonstrates the importance of this habitat for stream secondary production. In addition, the surface area covered by gravel and *Ranunculus* in many streams may well exceed that of marginal vegetation. The relative contribution of these habitats to the chalk stream invertebrate community as a whole may well exceed that of marginal vegetation, as a result.

As a result of the heterogeneity and equitability of margins, several different types of taxa can be found there:

1. Taxa that are intolerant of stagnant, still water, but are unable to live in fast-flowing mid-channel habitats with low structural complexity and high fish predation pressure. These taxa include the damselflies *Calopteryx splendens* (which oviposit preferentially in fast-flowing water – Gibbons & Pain, 1992) and *C. virgo*; some *Simulium* species that prefer stable, slow- flowing habitats and caddis that are associated with tree roots or vegetation in flowing waters, such as *Oecetis* sp. and *Mystacides azurea*. Some true bugs, beetles and snails are also relatively intolerant of still, stagnant water, yet live in vegetated habitats, possibly to avoid predation from fish. These include the bug *Micronecta poweri*, the beetle *Platambus maculatus* and the snails *Planorbis vortex* and *Valvata* spp. Stream margins represent the major, dominant habitat for many of these taxa.

2. Taxa that favour other habitats, but are also found in the margins in large numbers (such as baetid and ephemerellid mayflies, elmid beetles (particularly larvae) and snails such as

Potamopyrgus jenkinsi) because margins possess elements of these other habitats. Margins are thus a secondary, sub-dominant habitat for these taxa.

3. Taxa that use margins only temporally. This group includes:
   - taxa with larvae that spend the first part of their lives in margins, following adult oviposition (such as *Potamophylax* sp. and *Halesus radiatus* in this study),
   - taxa that use margins as a conduit between the aquatic and terrestrial environment,
   - taxa that use margins as temporary flow refugia during spates.

   Margins are thus a temporary but vital habitat for many of these taxa.

4. Taxa that are characteristic of still water, vegetated habitats, such as small pond and ditches. These taxa are typically widely distributed in locally discreet habitats within a flood plain and include many beetles, snails and true bugs. The winged adults of bugs and beetles may also move between these habitats, such that individuals in margins are part of a widespread metapopulation. Stream margins, although not the sole habitat, are thus a major co-dominant habitat for these taxa. Should small ponds and ditches dry up during a dry summer, stream margins may be a vital habitat for many of these taxa.

5. Taxa that are terrestrial or semi-aquatic and spend the majority of their lives in the vegetation at the water's edge. Such taxa include beetles that spend alternate parts of their life cycle in either the aquatic or terrestrial part of the marginal vegetation habitat. Examples are *Elodes* sp. (which has aquatic larvae and terrestrial adults) and *Helophorus* sp. (which has aquatic adults and terrestrial larvae). Stream margins are a major co-dominant habitat for these taxa.

In contrast to the different groups of taxa in marginal vegetation (which reflects the variability of the habitat) taxa found in gravel and *Ranunculus* tend to be solely specialists of these habitats. Due to the more extreme physical conditions of high flow and low habitat structure, taxa have to be well suited to these habitats to live there and are unlikely to include those normally found in other habitats.

A much greater number of 'rare' taxa were found in marginal vegetation, including many beetles and bugs. In other studies, stream margins have been found to contain taxa otherwise rare in the stream (Jenkins *et al.*, 1984). One possible explanation for this is the presence in stream margins of taxa that belong to a wider metapopulation of individuals living in still-water ephemeral habitats, such as ditches, small ponds and puddles distributed throughout the flood plain. Populations of these taxa in stream margins will thus reflect only a small proportion of the total population in a given area. In contrast, densities of taxa typical of *Ranunculus* or mid-channel gravel will be high, as populations will be confined locally to these habitats.

Marginal vegetation can also be vital for the reproduction of many stream invertebrates, including those normally found in other habitats. The significantly higher abundance of egg masses and adults in the margins indicated that this habitat was used as a site of oviposition by many taxa. The presence of adults in samples also indicated either that adults were entering the water along the margins to lay eggs, or were emerging from the water. Margins thus acted as a 'conduit' for many taxa with terrestrial adults and aquatic larvae. Stream sections without well-developed margins may have poorer recruitment of some aquatic insects as a result. Many beetle taxa are reported to pupate on dry land, usually only a few centimetres from the water's edge (Fitter & Manuel, 1986). The physical nature of margins may thus not only be important for beetles as they move onto dry land, but may itself reflect terrestrial conditions. Well-consolidated, vegetated margins may be more suitable for beetle pupation than silty, unstable grazed banks dominated by grasses, where soil conditions may be detrimental for beetle pupation. Artificial banks with no natural vegetation cover will also be unsuitable for beetle pupation.

The area of stream ecology where 'habitat' assumes the greatest importance is in the conservation and restoration of water bodies. Habitats are usually defined as visually distinct areas of different substrate type, physical structure, flow rate or depth (Barmuta, 1989; Palmer *et al.* 1991; Pardo & Armitage, 1997). It is difficult and expensive to manage streams and rivers either for individual species, or communities, with the exception of some large species of bird and mammal where there is already a large body of biological information. Discrete aquatic habitats, however, such as macrophyte beds, riffles and pools (the so-called 'building blocks for river conservation') (Harper *et al.* 1992) can be recognised by managers, engineering contractors and the informed public as well as biologists. Relative to the amount of information about the numbers and types of habitats in streams and what invertebrates are found in them, little is known either about the true ecological function of these discrete habitats, or how relatively important each habitat is. This study has demonstrated the high importance of stream margins to a chalk stream invertebrate community, relative to the mid-channel habitats of coarse gavel and *Ranunculus* beds. Although all habitats are inter-linked, physically and biologically and none can be considered independently of the others, conservation of such streams should focus on margins as centres of biodiversity, rarity and reproduction.

Stream restoration is the area of management activity where the concept of functional habitats has been most used (Harper *et al.* 1995). Such restoration has focused largely on the re-instatement of riffle-pool sequences (Friberg *et al.* 1994; Ebrahimnezhad & Harper, 1997; Harper *et al.* 1998, Friberg *et al.* 1998; Gortz, 1998), although other projects have emphasised the importance of macrophytes as invertebrate habitat in restored sections (Biggs *et al.* 1998). Given the importance of marginal vegetation in this study, greater emphasis needs to be given to this under-studied habitat in restoration programmes. In particular, any project that destroys well-developed marginal vegetation in order to 'improve' the mid-channel substrate may reduce, rather than improve the conservation value of the stretch. Re-creating the hydraulic regime and physical bank conditions where marginal vegetation can flourish should also assume a greater importance in stream restoration projects than it has hitherto been given. Encouraging the rapid return of natural marginal vegetation in sections of stream that have been re-sectioned or have been re-dug into a more natural, meandering course (Biggs *et al.*, 1998) is likely to allow quicker recovery of diverse and abundant macroinvertebrate communities.

4.5 Summary

- Semi-quantitative invertebrate samples were taken from three habitats: mid-channel gravel, *Ranunculus* and marginal vegetation, in six lowland chalk streams, on four sampling occasions between May 1996 and January 1997.

- In comparison to seasonal effects, little difference was found between invertebrate communities in different types of marginal vegetation. The characteristic features of most marginal vegetation included high structure, abundant detritus, periphyton and other plant-derived food and low flow. The aquatic invertebrate assemblages found in the trailing stems and leaves of overhanging terrestrial vegetation were as abundant and taxon-rich as those found in semi-emergent marginal macrophytes.

- The invertebrate assemblages in marginal vegetation, *Ranunculus* beds and in mid-channel gravel could be distinguished from each other over most of the year, particularly in spring and winter. Taxon richness was generally higher in the margins, although invertebrate abundance per sample was highest in *Ranunculus*, due to the high numbers of mayfly and blackfly larvae.

- Over half of all taxa identified on each sampling occasion showed a significant difference in abundance between habitats. Of these taxa, many more were found in the marginal vegetation, compared to gravel or *Ranunculus*. Significantly greater numbers of egg masses and adult insects (either emerging from the water or ovipositing in water) were found in marginal vegetation, also demonstrating the value of this habitat for reproduction and recruitment of aquatic insects.

- For each taxon, the mean proportion of its population in each of the three habitats was calculated. The overall mean proportion per taxon in each habitat was greatest for marginal vegetation, and least for *Ranunculus*, with gravel intermediate. This indicated that for the invertebrate community as a whole, margins were relatively more important for taxa than either gravel or *Ranunculus*. In addition, many more taxa avoided gravel and *Ranunculus* than avoided margins, over all four sampling occasions.

- The physical diversity within marginal vegetation, including elements of other habitats, allowed different invertebrate groups to live there. These included:
  a) taxa normally restricted to lotic margins,
  b) taxa typical of other stream habitats but occasionally found in margins,
  c) taxa using margins as a temporary habitat or refuge,
  d) taxa normally found in still-water habitats, such as ditches and small ponds,
  e) taxa spending only part of their life cycle in aquatic habitats.
  In contrast, gravel and *Ranunculus*, which experienced high flow, comparatively low structural diversity, and potentially high predation pressure, were colonised by specialist taxa.

5. THE INFLUENCE OF TREES ON THE REPRODUCTION & RECRUITMENT OF THE CADDIS *AGAPETUS FUSCIPES*

5.1 Introduction

The ecology of aquatic insects is widely assumed to be determined solely by aquatic factors, both biotic and abiotic (Hildrew & Townsend, 1987). Recent research, however, has demonstrated the importance of terrestrial adults in the distribution, abundance and population dynamics of aquatic larvae (Enders & Wagner, 1996; Bunn & Hughes, 1997; Harrison & Hildrew, 1998). Riparian vegetation is known to be an important factor in the ecology of adult insects (Sweeney, 1993; Collier & Smith, 1998; Harrison & Hildrew, 1998). Very few studies have looked at the link between terrestrial vegetation, adults and larvae, although adult swarming and oviposition near to bankside trees and reeds has been shown to be a major determinant of the distribution of larvae of lotic caddis flies (Statzner, 1977).

This investigation concerns the distribution of the common and abundant cased caddis *Agapetus fuscipes* Curtis (Glossosomatidae) in chalk stream tributaries of the rivers Frome and Piddle in Dorset, UK. Taxa are often recorded in streams with an abundance which, although not rare, is low enough to prevent any but tentative conclusions being made concerning habitat preference. Using such taxa it is also extremely difficult to determine which factors influence their distribution and which do not. However, single-species studies using abundant taxa such as *Agapetus* allow greater concentration of effort, and the chance to carry out much more detailed surveys than would otherwise be possible.

The study began with a survey of aquatic invertebrates from the mid-channel gravel of short (50-200m) stream sections, which differed in their riparian vegetation characteristics. Initial observation and sampling results suggested that *Agapetus* would be suitable for study alone, by virtue of the great abundance of larvae and adults, and the seemingly strong influence of riparian trees on it's distribution. In some wooded reaches larval cases could be seen entirely covering the mid-channel gravel, whilst absent in such numbers elsewhere. It was thus thought highly likely that a significant relationship would be detected between this caddis and riparian habitats. This would, it was envisaged, provide an insight into the factors affecting the distribution of other aquatic holometabolous invertebrates, and produce implications for the management of riparian and marginal areas. Thus, an intensive investigation of the distribution and abundance of adults and larvae of this species with respect to bankside trees, across three separate headwater streams, was carried out.

5.2 Methods

5.2.1 First year study

Six headwater chalk streams (see Table 2.1, page 4) were selected for study. Each stream possessed similar hydrological and physical properties (0.3 –0.6m max. depth, 4.5 – 8.5m width) and each had short (50-200m) sections characterised by different bankside vegetation growth, due to changes in management regime. Vegetation was classified as either:

- 'grazed' -short grass (accessible to cattle),
- 'ungrazed' - abundant herbs, shrubs and occasional trees (fenced from cattle),
- 'woodland' - closed-canopy deciduous trees on both banks (fenced from cattle).

15-second invertebrate kick-samples were taken from the mid-channel substrate (compacted coarse gravel and flints) of each section. Again, three patches of similar flow regime and substrate size were sampled in each section and combined to give a mean sample per section. Terrestrial adult aquatic insects were sampled from the bankside vegetation of each section, using a sweep net (3 x 30sec sweeps). All invertebrates were preserved, sorted, identified and counted in the laboratory to the highest possible taxonomic group. Aquatic samples were taken at the same sites in May, July, September 1996 and January 1997. Terrestrial samples were taken in May, July and September 1996.

5.2.2 Second year study

Three streams from the first part of the study were selected for more intensive investigation (Bere stream, Tadnoll brook and a tributary of the Piddle at Waterston). Each stream-reach investigated flowed through a woodland section directly into an open section with only sparse riparian vegetation. *Agapetus* larvae were sampled at three mid-channel sites along each stream:

a) shaded sections in the woodland ('Under trees')
b) approx. 50m downstream from the woodland in the open section ('Near trees')
c) 100-200m downstream from the woodland in the open section ('Away from trees').

The different sections along each stream had similar physical characteristics including flow rate and substrate size. Three samples were taken at each site using a 30cm x 30cm benthic Surber sampler. Following preservation in 70% alcohol, larvae were identified, assigned to five size classes (rather than instar, of which there are reported to be as many as eight – Castro, 1975) and counted in the laboratory. Eggs-masses, deposited directly by submerging adults onto small pieces of gravel in mid-channel (Anderson, 1974), were also counted. Adults were sampled using Malaise traps (Plate 5.1) placed on the bank at the three sites (one per site) along each stream. The investigation ran from May 1997 through to January 1998, with samples taken bi-weekly, then monthly after July. Due to excessive weed growth in one stream (Tadnoll brook) no samples were taken at the Near trees site in this stream, after the first sampling occasion.

Plate 5.1: A malaise trap in position at Waterston. Summer 1997.
This trap and others were fenced, as shown, to prevent damage by livestock

Plate 5.2: An 'open' stretch, looking upstream, at Waterston.
The wooded section of this particular site can be seen beyond.

5.3 Results

In the first year's study, *Agapetus* larvae were very much more abundant in woodland sections than either grazed or ungrazed sections, particularly in July (Fig. 5.1a, Table 5.1). Numbers of larvae declined rapidly, such that there was little difference between sections in January. There were significant differences between sections in the abundance of adults, with particularly large numbers in woodland in May. Very few adults were found in short, grazed vegetation (Fig. 13b, Table 22).

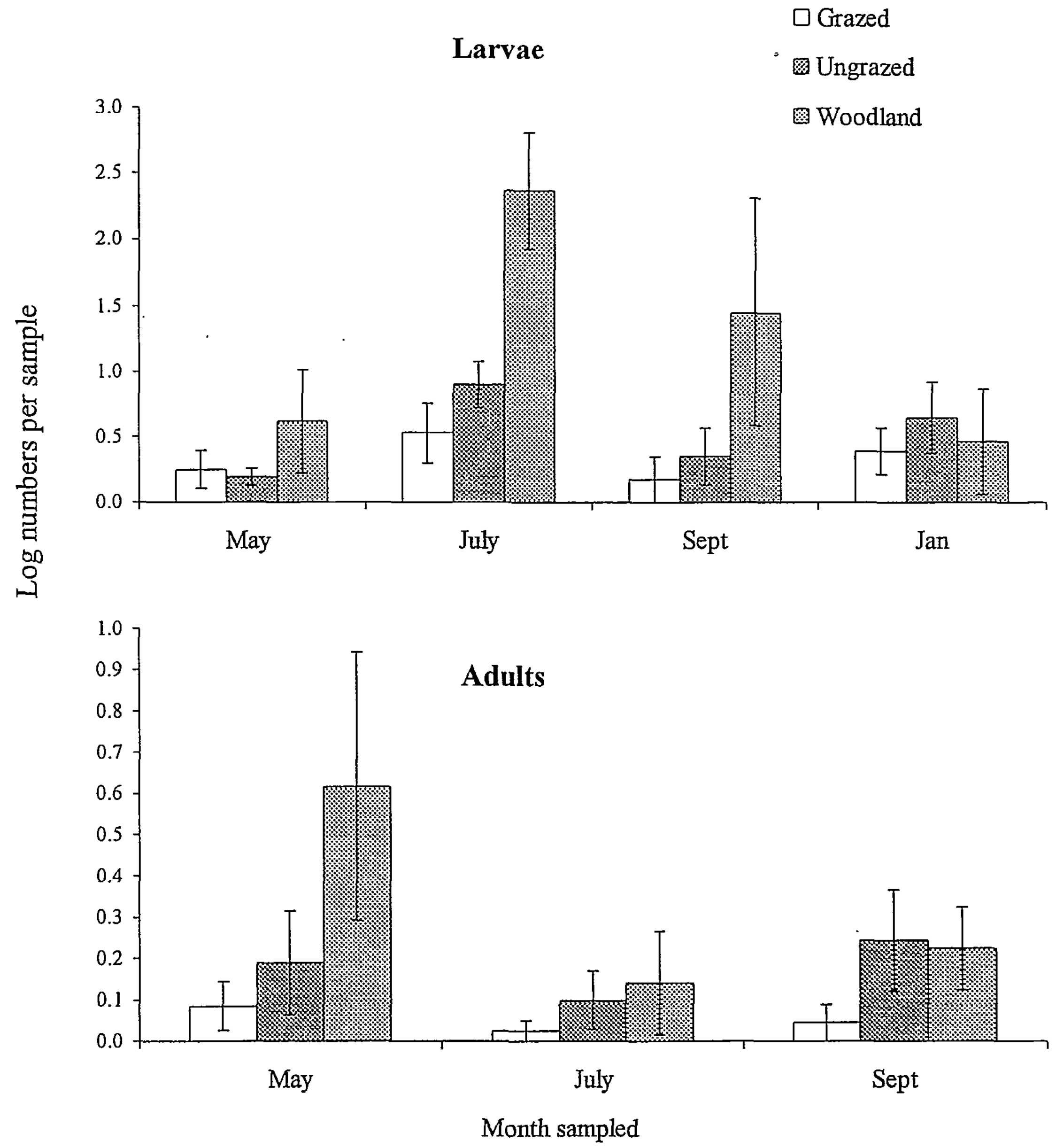


Figure 5.1a & b Abundance of larval (top panel) and adult (bottom panel) *Agapetus fuscipes* between three sampling regimes (woodland, ungrazed/fenced and grazed), from sweep-net samples taken during May, July and September.

In the second year's study, larvae of all size classes and egg masses showed significant differences between habitats and were most abundant in open sites near trees (Fig. 5.2, Table 5.2). The abundance of larvae under trees relative to other sites changed as larvae grew,

Table 5.1 Results of a two-way ANOVA of larvae and adult abundance (log-transformed) with Habitat (grazed, ungrazed and woodland) and Season as main factors. *** = P<0.001 ** = P<0.01 * = P<0.05

Factor	DF	Larvae		Adults	
		F	P	F	P
Habitat	2, 44	9.369	< 0.001***	3.565	0.040*
Season	3, 44	6.257	0.001**	2.317	0.114
Habitat x Season	6, 44	2.119	0.070	1.128	0.360

Table 5.2 Results of a two-way ANOVA of larvae and egg mass density (log-transformed) with Habitat (under trees, near trees and away from trees) and Time (date sampled) as main factors. *** = P<0.001 ** = P<0.01 * = P<0.05

Factor	DF	Egg Mass		Size Class 1		Size Class 2		Size Class 3		Size Class 4		Size Class 5 + Pupae	
		F	P	F	P	F	P	F	P	F	P	F	P
Habitat	2, 45	7.053	0.002**	9.789	<0.001***	14.075	<0.001***	12.077	<0.001***	8.134	0.001**	6.237	0.004**
Time	8, 45	5.509	<0.001***	1.886	0.086	7.298	<0.001***	5.202	<0.001***	1.998	0.069	0.857	0.559
Habitat x Time	8, 45	0.556	0.892	0.619	0.851	1.544	0.783	0.522	0.921	0.371	0.983	0.594	0.872

Table 5.3 Results of a two-way ANOVA of adult density (log-transformed) with Habitat (under trees, near trees and away from trees) and Time as main factors. *** = P<0.001 ** = P<0.01 * = P<0.05

Factor	dF	Adults	
		F	P
Habitat	2, 60	6.908	0.002**
Time	9, 60	3.450	0.002**
Habitat x Time	18, 60	0.704	0.793

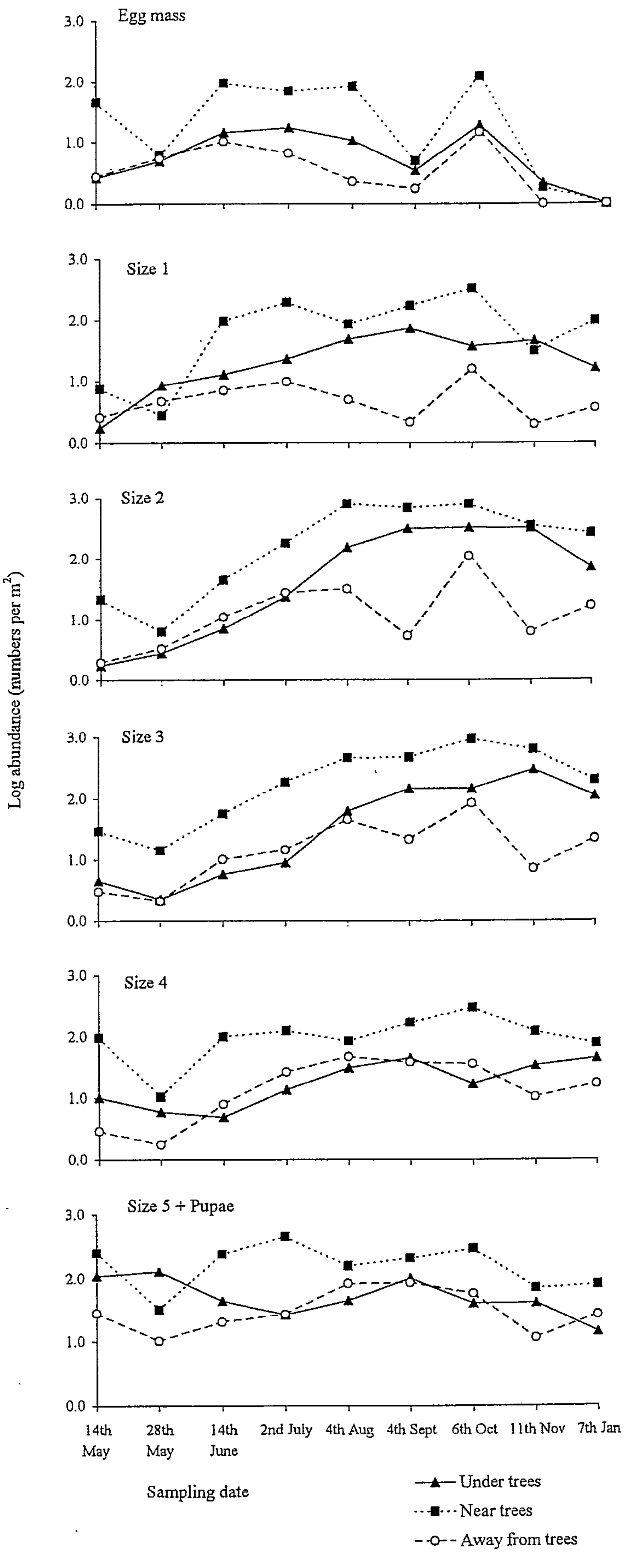


Figure 5.2: The distribution and abundance of *Agapetus fuscipes* egg masses and larval size classes in three habitat regmes, woodland (under trees), near trees and away from trees (open field), over the period 14th May 1997 to 7th January 1998. Note log-Abundance .

however. Tukey post-hoc tests of pairwise differences between habitats showed that size classes 1 and 2 were significantly ($P<0.05$) more abundant under trees compared to away from trees. There were no significant differences between these two habitats in larger size classes or in egg masses. The distribution of adults showed a similar distribution between sites as that of larvae. Significantly more adults were always caught in Malaise traps near trees compared to away from trees, over the course of the experiment (Fig. 5.3, Table 5.3; Tukey post-hoc test of pairwise differences between habitats: $P<0.05$). Numbers caught in woodland traps showed considerable temporal variation.

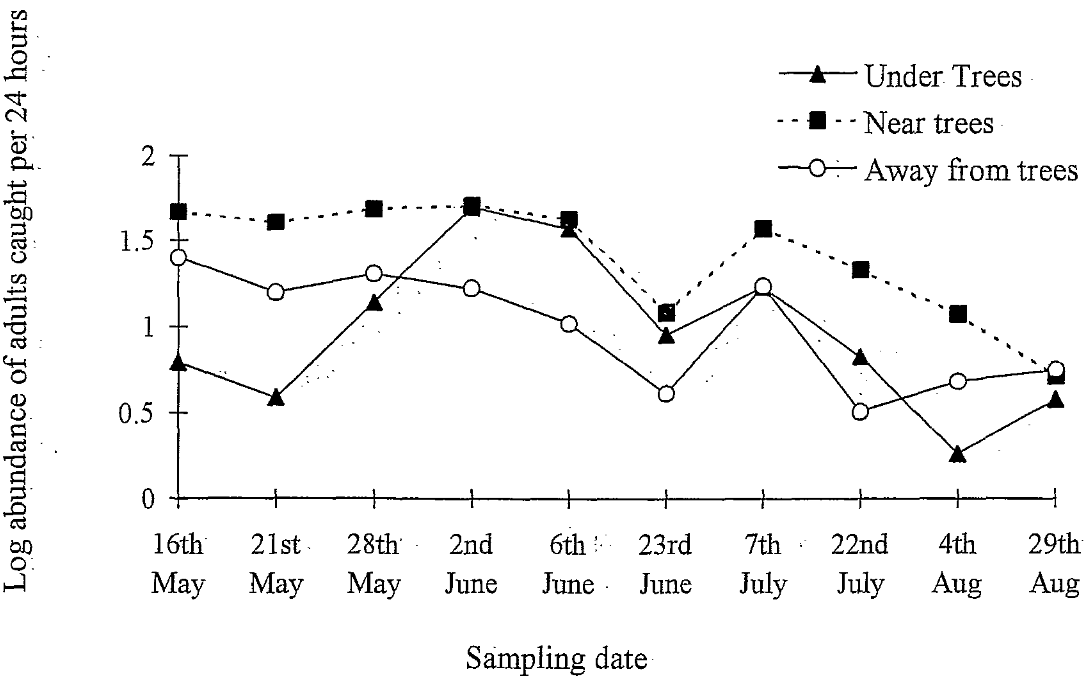


Figure 5.3. The distribution of *Agapetus fuscipes* adults between three habitat regimes (wood, near trees, and away from trees) collected using Malaise traps between May and August.

A large number of other adult invertebrates were caught in the Malaise traps at the same time as *Agapetus*. Principally, these included another 26 species of caddis, although various other taxa (mayflies, stoneflies, alderflies and tipulids) were also captured. The distribution, abundance and diversity of the caddis caught in this experiment are presented in the next chapter.

5.4 Discussion

The strong recruitment of *Agapetus* larvae in woodland evident from the first year's survey, together with the greater number of adults found in this habitat, indicate that either aquatic conditions in woodland were favourable for larvae, or that adults favour the terrestrial habitat in and under trees. The former is unlikely to be true. Larvae are reported to eat benthic diatoms and organic detritus (Castro, 1975), both of which are likely to be limiting in woodland sections. In-stream macrophytes (mainly *Ranunculus* sp. and *Apium nodiflorum*) provide much of the organic debris in chalk streams (Dawson, 1976) and are much less abundant in shaded parts of streams. Macroinvertebrate production has been frequently shown to be lower in forested streams, due to the low growth of periphyton (Behmer & Hawkins, 1986; Sweeney, 1993). Other than light levels, physical conditions such as flow rate, temperature and substrate size were similar across all sections, within each stream due to both the short length of each section and to the relative independence of groundwater-fed chalk streams from terrestrial riparian conditions (Berrie, 1992).

In the second year's investigation, the greater abundance of the egg masses and small size-class larvae under trees and particularly in open sites near trees, indicated that larvae were recruited in these areas, following adult oviposition. The lack of persistence of larger larvae under trees indicated that larvae dispersed downstream into open sites as they grew, consistent with the idea that shaded sites are unsuitable for larval growth. Larval drift is reported to be common in this species (Wallace, 1991) and may be a general response of larvae moving away from unsuitable sites, following adult oviposition.

Adult oviposition choice with respect to trees thus set an initial patchiness (or 'oviposition fingerprint') of distribution of *Agapetus fuscipes* larvae, as has been described for other lotic and lentic caddis (Statzner, 1977; Harrison & Hildrew, 1998). Adults clearly had an association with trees, although they were more common at the woodland edge, rather than in woodland itself (as were larvae). This may represent either a true distribution of more adults always found near trees, or may be due to a degree of sampling error. Sampling techniques using Malaise traps may bias the numbers of adults caught, as traps in the open may function as surrogate trees or bushes and thus attract caddis (although both traps in the open sites would act in a similar manner). Adults may also fly less in woodland compared to open habitats and so be caught less in Malaise traps that catch adults on the wing. Adults may associate with trees for many reasons, including using them as shelter from predators, wind or desiccation and as swarm markers (Statzner, 1977; Sweeney, 1993; Collier *et al.*, 1997). Riparian vegetation can also provide food for adults, to provide energy for flight or ovarian maturation (Jones 1974; Sweeney, 1993; Petersson & Hasselrot, 1994).

Riparian vegetation type and structure has been found to be a major factor in the distribution and abundance of adult caddis along or between streams (Collier *et al.*, 1997). Very few studies have linked the distribution of aquatic larvae with that of adults, although recent research on the ecology of adult aquatic insects has demonstrated their importance in the abundance and distribution of aquatic larvae (Enders & Wagner, 1996; Bunn & Hughes, 1997; Harrison & Hildrew, 1998). In this investigation, there may even have been considerable conflict between adult and larval survival. Very low persistence of larvae in woodland sections, despite the high recruitment, suggests that adults may have maximised their own survival, at the expense of their larvae, in a similar manner to that postulated for littoral caddis and chironomids (Harrison & Hildrew, 1998). Dispersal to open sites may have enabled larvae to escape intense competition for limited food resources, but would have led to greater costs associated with dispersal, including predation, lower feeding rate and construction of new cases.

It cannot be stated with certainty that the findings relating to *Agapetus* obtained from this investigation can be applied to other species of invertebrate with terrestrial adults, or even other caddis. Predatory caddis larvae, for example, are unlikely to be dependant (directly at least) on 'open' stretches of stream to provide food, as is the case for grazing *Agapetus* larvae. Such caddis may not require the same range of habitats as *Agapetus,* as adult and larvae may be able to share a mono-specific stretch of stream. It is however highly likely that many if not all emergent adults will be subject to the same pressures (e.g. predation, desiccation, the need for swarm markers and oviposition sites), and therefore it is also unlikely that *Agapetus*' strategy and behaviour is unique. Personal observation and sweep-net samples revealed the rapid redistribution of *Potamophylax* (a limnephilid) adults away from open areas as the sun rose and the dew evaporated. The close proximity of different types of habitat may thus be required solely by the adult (rather than by the adult and the larvae) of some species or genera. Other species, chiefly caddis, are discussed in the Section 6, although none were as surveyed as intensively, or were as abundant, as *Agapetus.*

5.5 Conclusion

This study has demonstrated the importance of local riparian vegetation structure and management on the distribution of *Agapetus fuscipes* larvae. *Agapetus* evidently needs both suitable aquatic habitat for larvae and terrestrial habitat for adults in order to flourish in any particular water body, as has been postulated for aquatic insects with terrestrial adults in the past (Macan, 1961). Potentially, therefore, changes to the riparian landscape could have important consequences for invertebrate abundance and diversity in streams, via its effect on terrestrial adults of this and other species. This is likely to have greatest impact in areas where riparian vegetation has been extensively modified or removed, such as intensively farmed areas or deforested uplands.

6. THE INFLUENCE OF RIPARIAN VEGETARIAN ON ADULT AND AQUATIC INSECTS

6.1 Introduction

In order to complement, and expand upon, the *Agapetus* work carried out during the summer of 1997, a suite of experiments was devised to investigate the distribution of larval and adult invertebrate stages. Part of the first and second years' work had revealed and demonstrated, respectively, a link between terrestrial vegetation and invertebrate distribution. This was indicated by *Agapetus*' apparent requirement for woodland (in the first instance) and in particular the interface between woodland and open-areas. At that time however, the malaise traps were identified as a possible source of bias to the data, given that they had the potential to function as surrogate bushes. Accordingly, one of the prime considerations of the new sets of experiments was that they were non-intrusive in nature.

The investigation aimed not only to assess the requirement of other adult insects for distinct vegetation types, but also to go some way towards demonstrating the relative importance and dependence that various adult taxa place upon each riparian zone. Some of the work is preliminary in nature, and time constraints largely determined the extent of data collection and analysis. Extra sampling occasions, plus family- and species-specific data analysis (as for *Agapetus*) would be required were the subject to be taken further.

The study was conducted on a section of stream that flowed from a small, broad-leaved woodland area straight into an open, treeless zone (Plate 6.1). This open section consisted of a gravel track with short sward on one side and taller herbs on the other. By using several terrestrial and aquatic sampling techniques it was possible to determine the relative importance of both types of bankside regime to a wide variety of both adult and larval invertebrate taxa.

6.2 Methods

6.2.1 Sites

The sites where Malaise traps were set-up during 1997 is described in Section 5.2.2 (page 72). Three streams were used: The Tadnoll Brook near Warmwell, the Bere Stream at Roke Farm (above Bere Regis) and a tributary of the Piddle at Waterston.

In 1998, work was carried out on one stream section - the Bere Stream at Roke Farm. This section of stream was some 100m downstream of the Bere Stream site described in section 7.2.1., and covered the same area as the Malaise traps from 1997. The site was entirely suitable, both in terms of vegetation management and invertebrate populations, and offered unrestricted access to both stream and banks. It was also clean, and safe from human and livestock disturbance.

This upper reach of the Bere stream provided a suitable site due to its stable flow and shallow, uniform profile. The entire reach consisted of approximately 150 metres of stream, which comprised two sections: woodland and open. The woodland section was the upstream of the two, and occupied approximately 50m on one bank, with the remaining 100m being the downstream 'open' section. In the 'open' section, the tall herbs plus the dead and emerging vegetation that was present on one bank were cleared at the start of the experiment. No further management of this nature was undertaken on either section during the experimental period, although *Ranunculus* was removed in July by the cress-farm.

Plate 6.1: The Bere Stream, summer 1998. Looking upstream from the 'open' section to the 'wooded' section.

6.2.2 Sampling techniques

Summer 1997

As described in section 5.2.2, Malaise traps were used to record the distribution and abundance of adult *Agapetus fuscipes* in relation to open and wooded areas (in 1997). The traps collected many other caddis in addition, and these data are provided in this chapter. Sampling took place between May and August, on nine occasions (16/05/97, 23/05/97, 30/5/97, 02/06/97, 09/06/97, 26/06/97, 07/07/97, 22/07/97 and 06/08/97) from sites which had open areas adjacent to sections of woodland.

Summer 1998

Over the course of the summer, four suites of experiments were conducted on the Bere Stream reach. The overall purpose of these experiments was to elicit the effect(s) that the two blocks of contrasting vegetation types had i) upon the distribution of the terrestrial adults (both on a daily basis and long-term) and ii) upon the distribution of the aquatic larvae. The experiments are described:

- Sticky trapping: A4-size acetate sheets were coated with a specialist, non-toxic, non-drying insect adhesive (Oecotak) and wrapped around sections of 7cm-diameter drainpipe. These drainpipe sections were fastened to wooden stakes which held them approximately 1½ -2 feet off the ground. This arrangement was replicated 6 times in each of the two stream sections, and was repeated 4 times over the course of the summer (19/05/98, 19/06/98, 12/08/98 and 11/09/98).

- Drift trapping: Drift traps were secured to the streambed with iron stakes, at the downstream end of the woodland and approximately 3/4 of the way down the open section. The traps were suspended approx. 2-3 cms above the streambed, and there was initially sufficient water within the stream to keep the traps completely submerged. Four traps were placed in each section, and the experiment was duplicated twice (20/05/98 and 15/06/98). The water level fell to such an extent after the *Ranunculus* was cut in July that it was no longer possible to achieve a suitable flow into the traps.

- Sweep netting: Samples were collected on two occasions (06/07/98 and 13/08/98) from the terrestrial vegetation present at each stream section. In the woodland this consisted of the lower aerial parts of the trees, and the under-storey of long grass and tall vegetation. In the open the vegetation included mainly nettles, grasses, young *Oenanthe* and emergent reeds. In addition, the field downstream of the open section was sampled. Although electrically fenced, grazing cattle were able to keep all bankside vegetation cropped very short. As a result, instream-*Apium* and short grasses were the dominant emergent plants. On both occasions four samples were taken in the morning (approx. 9.00am), four at noon (between 1-2pm) and four in the late evening (after 10pm), from each section.

- Surber sampling: Four benthic gravel samples were taken on four separate occasions (19/05/98, 15/06/98, 11/08/98 and 11/09/98) from each of the two sections (woodland and open). The four samples were taken randomly from just the one habitat in each section – that of clean gravel. At least half the length of the individual sections was covered each time.

6.3 Results

6.3.1 Malaise Traps (1997)

Chapter 5.0 was devoted to the most abundant adult caddis caught over the sampling period – *Agapetus fuscipes*. The very high numbers of adults, larvae and egg-masses of this species made it possible to piece together an overview of life-history requirements for this species. This was an intensive investigation, and was not replicated for other species.

However, the range of other adult caddis caught demonstrated significant differences in behaviour as a result of the contrasting management regimes (Fig. 6.1).

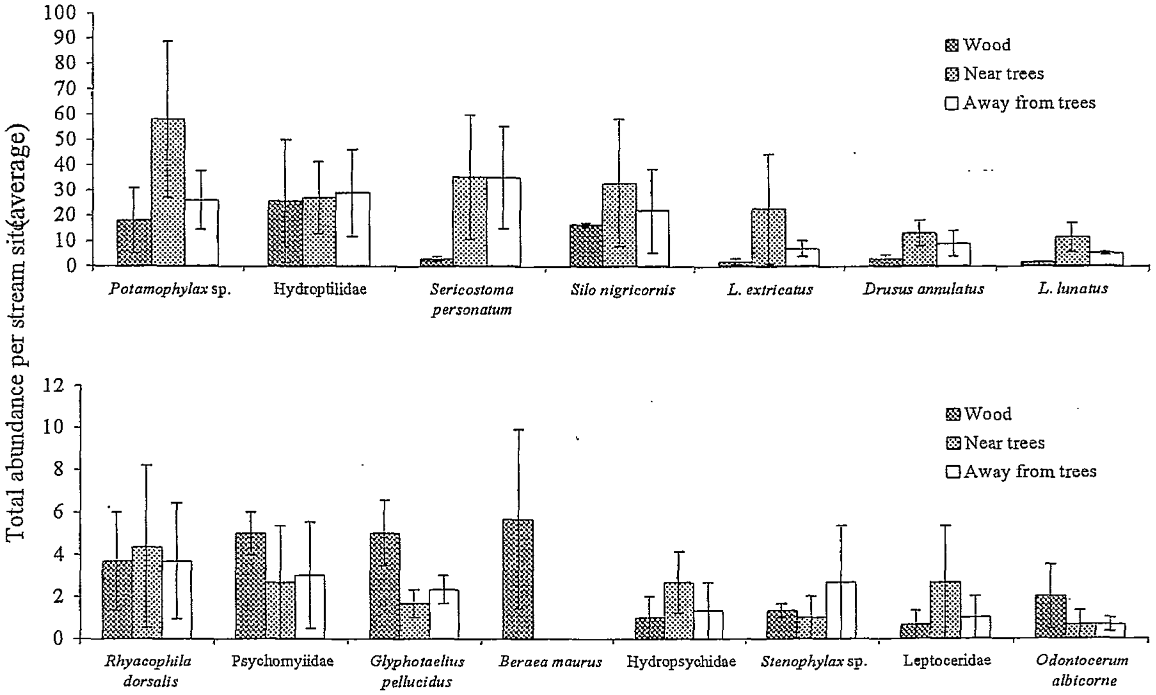


Figure 6.1. Malaise trap results for caddis abundance, taken from three regimes - wood, 'near-trees' and 'away from trees', on nine occasions between May and August 1997, from three stream sites. Mean ± 1 S.E.

Some caddis are clearly influenced by various types of terrestrial vegetation, and for others terrestrial vegetation would seem to make little or no difference to their distribution. *Beraea maurus*, *Glyphotaelius pellucidus* (a limnephilid) and *Sericostoma personatum* are examples of the former group, whilst *Rhyacophila dorsalis*, Hydroptilidae and Psychomyiidae belong to the latter. Caddis such as *Limnephilus extricatus*, *Silo nigricornis* and Leptoceridae showed distinct preferences for certain habitats, but low abundances elsewhere meant overall distribution could not be statistically linked to any particular area.

Caddis diversity between the three different regimes (wood, near trees, away from trees) was very similar, as a mean of the three streams (Bere Stream, Tadnoll Brook and the Piddle at Waterston). In each case, the samples from either the woodland or 'near-trees' traps generally recorded a larger number of species than the 'away from trees' traps, although this was not statistically significant on any occasion (Table 25).

Table 6.1. Total adult Caddis diversity from the three stream sites, recorded between May and August 1997 from each regime (wood, near trees and away from trees).

	Woodland	Near Trees	Away from trees
Agapetus fuscipes	✓	✓	✓
Potamophylax sp.	✓	✓	✓
Limnephilus lunatus	✓	✓	✓
L. extricatus	✓	✓	✓
L. sparsus	✓	✓	✓
L. flavicornis		✓	
L. auricula	✓	✓	
L. hirsuitus		✓	✓
Limnephilus indet.	✓	✓	✓
Glyphotaelius pellucidus	✓	✓	✓
Halesus sp.		✓	✓
Stenophylax sp.	✓	✓	✓
Drusus annulatus	✓	✓	✓
Apatania muliebris	✓		
Silo nigricornis	✓	✓	✓
Silo pallipes			✓
Goera pilosa		✓	
Odontocerum albicorne	✓	✓	✓
Sericostoma personatum	✓	✓	✓
Plectronemia conspersa	✓	✓	
Psychomyiidae	✓	✓	✓
Rhyacophila dorsalis	✓	✓	✓
Hydropsychidae	✓	✓	✓
Hydroptilidae	✓	✓	✓
Leptoceridae	✓	✓	✓
Beraea pullata	✓		
Beraea maurus	✓		
Total	22	23	20

6.3.2 Sticky Traps

The sticky-traps revealed important differences in the distribution of several taxa between the woodland and open areas (Fig 6.2). Most notable amongst these were Baetidae, *Drusus*, Simuliidae and Sialidae, which were all more abundant in the open stretch. Several other taxa showed consistent differences between the two management regimes but not at a significant level, these were Tipulidae (more common in the open), Caenidae and Nemouridae (both more common in woodland). Many taxa showed no difference in their abundance on sticky traps between the two regimes despite contrary evidence from Malaise experiments (e.g. Chironomidae and *Agapetus*).

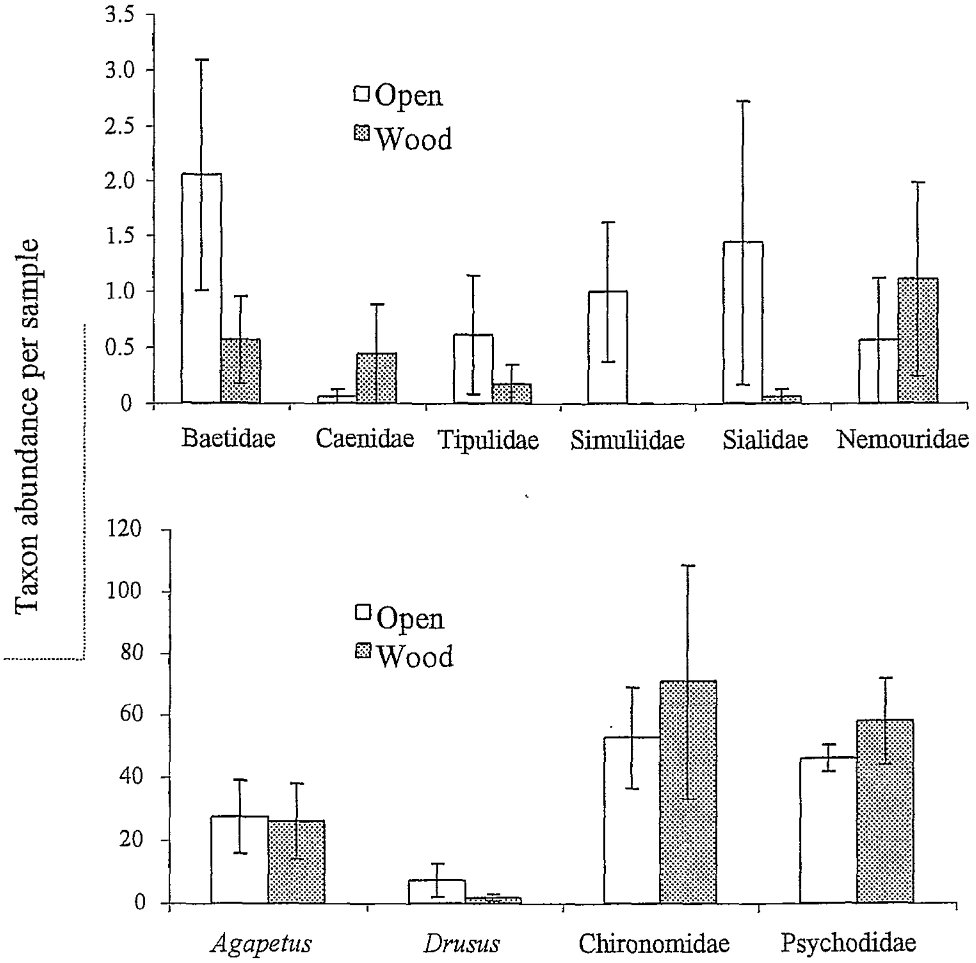


Figure 6.2. Results of sticky traps samples taken from each regime ('open' and 'wood') on four occasions between May and August 1998, six samples per occasion. Mean ± 1 S.E.

No significant difference in total adult abundance between management regimes was recorded on any of the four sampling occasions throughout the summer. The numbers of insects caught in both the woodland and the open sections matched each other very closely during this period, with peak abundances occurring in June (over 1000 flies/A4 acetate-sheet). Total adult diversity was, however, significantly greater in the open section in May and September, largely due to small numbers of Diptera (Tipulidae and Simuliidae), caddis (Sericostomatidae and Rhyacophilidae) and Sialidae.

6.3.3 Sweep-net samples

These samples showed a strong diel movement of chironomids and psychodids between the woodland area and the open reaches (open and 'field'). Psychodid abundance increased dramatically in the woodland reach in the evening, from a near zero level during the daytime sweeps to a mean of over fifty flies per sample in the evening (Fig. 6.3, top panel). Chironomid abundance in woodland showed a similar increase in the evening, albeit not so striking (Fig. 6.3, bottom panel). This evening increase was mirrored by a decrease in chironomid numbers in the grazed field – a regime that demonstrated very high numbers of chironomids at all times.

Other patterns were also observed. *Drusus* increased in abundance in the evening in both the open and the woodland reach, suggesting a general preference for activity at this time irrespective of vegetation. Conversely, *Agapetus* numbers peaked at noon in similar numbers in all three reaches; wood, open and field. Culicidae abundance during the daylight hours remained low in all three reaches, then showed a large increase in the field in the evening. (This accords well with the adult dispersal described by Cranston *et al.*, 1985). Tipulidae abundance remained at similar levels for all three reaches throughout the morning to evening period, with greatest abundance recorded from the wooded reach. (Fig. 6.4).

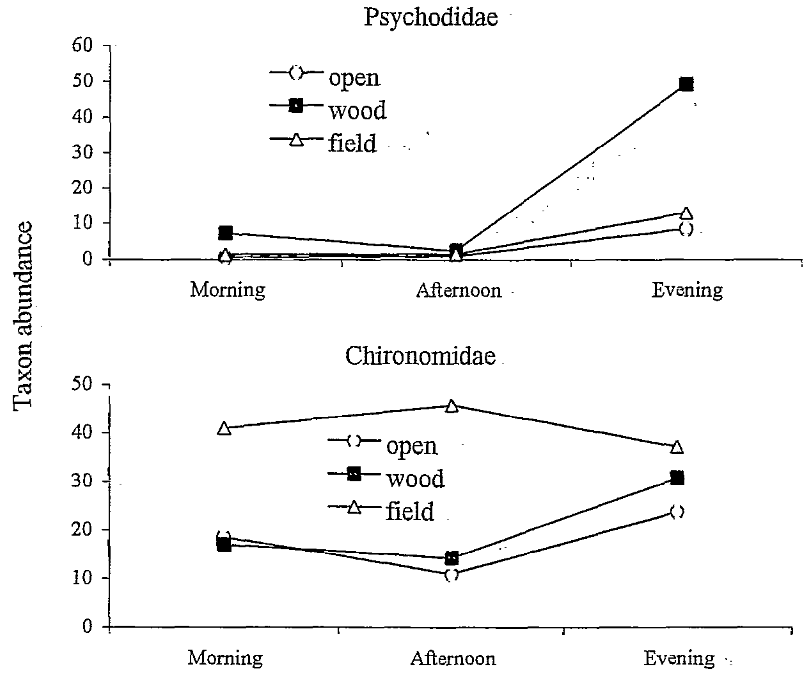


Figure 6.3. Diel variation of psychodids and chironomids between three habitats ('wood', 'open/ungrazed' and 'field/grazed') on two occasions between June and August 1998.

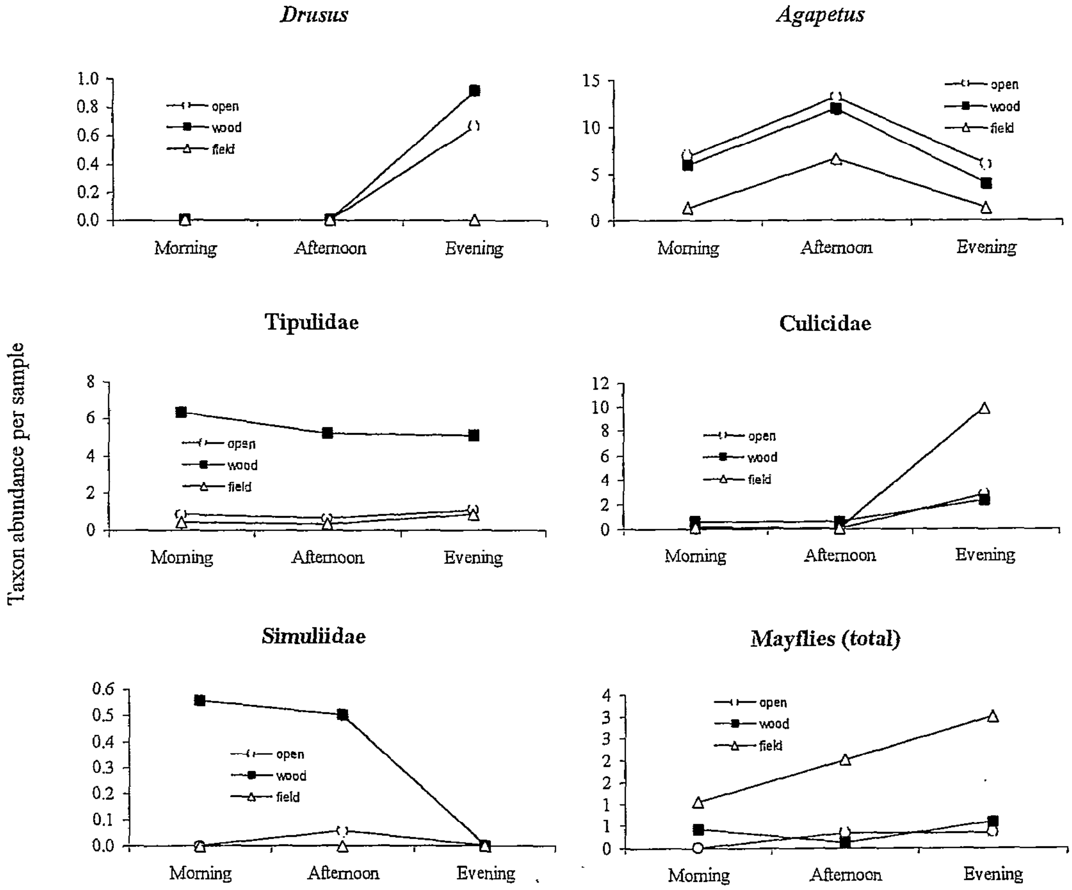


Figure 6.4. Diel variation of various taxa between three habitats ('wood', 'open/ungrazed' and 'field/grazed') on two occasions between June and August 1998.

The above graphs demonstrate interpolated diel trends in adult invertebrate distribution. The data is insufficient to allow an exact representation for each species and family, but given the short period over which the samples were taken it is likely that these graphs represent genuine observable patterns. In some cases the recorded abundances were so low (e.g. Simuliidae) that more work would be required to substantiate any conclusions drawn from the graph alone.

6.3.4 Surber samples

Surber samples from clean gravel alone, in both the woodland and open/ungrazed reach, demonstrated a difference in the abundance of several taxa (Fig. 6.5). Caddis as a group in particular showed distinct preference for the wooded reach, with significantly larger numbers of Sericostomatidae, Rhyacophilidae, Goeridae and Odontoceridae found there rather than in the open stretch. The abundance of Simuliidae and Caenidae was also higher in the woodland stretch, in contrast to the Baetidae and especially the Chironomidae, which were very much more abundant in the open section. Taxa showing little or no difference between the two reaches included *Agapetus*, *Drusus*, Ephemerellidae and some diptera (e.g. Ceratopogonidae, Empididae and various pupae).

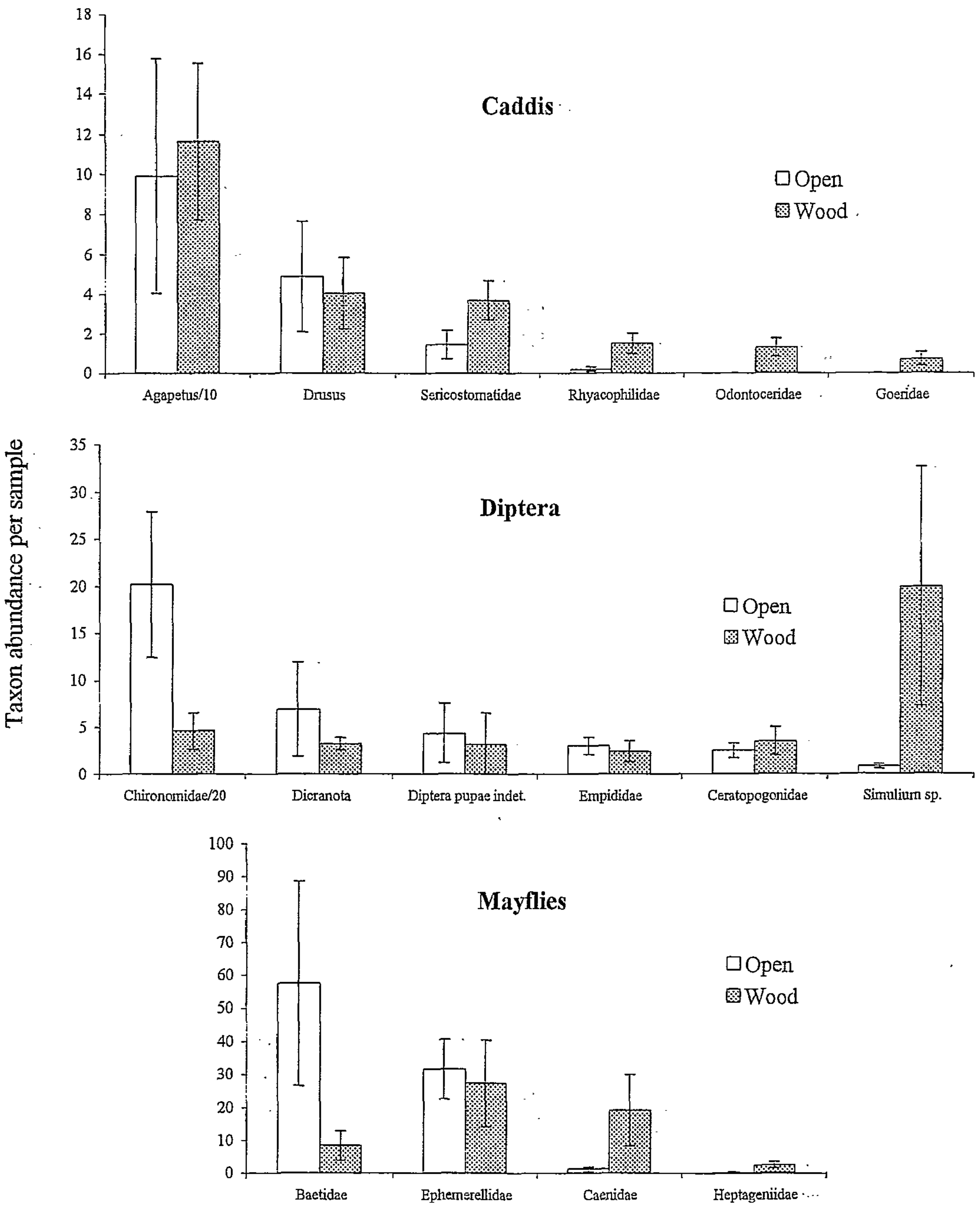


Figure 6.5. Results of the Surber-sample survey, conducted in the two reaches ('open' and 'wood') on four occasions (May, June, August and September 1998). Mean ± 1 S.E.

6.3.5 Drift Traps. Due to low-flows within the stream during and after July the drift traps were only operational twice. However, similar differences were detected on both occasions in the numbers of certain taxa drifting within the two reaches (Fig. 6.6). Chief amongst these were Chironomidae, with over four times as many chironomids drifting from the open area than from the woodland area. This accords well with the number of chironomids taken from each reach by the Surber sampler (section 6.3.3). Ephydridae, unidentified dipteran pupae and baetids were also found to drift in greater numbers in the open reach than in the woodland reach. This is not surprising in the case of baetids, which were recorded in much higher numbers on the substrate of the open stretch using the Surber sampler. The high numbers of ephydrid pupae caught in 'open' drift traps, in combination with the lack of these same pupae recorded in either stretch by Surber sampling (from benthic gravel) suggests that they are concentrated in open marginal areas. Table 4.12 ('Rare Taxa' – page 63) also indicates that Ephydridae, although apparently scarce, prefer marginal areas. Unfortunately no data was recorded for adult ephydrid distribution, due to constraints on time. The numbers of Simuliidae larvae caught drifting showed no difference between the two reaches despite the larvae being dramatically more abundant in the woodland. Ephemerellidae showed a small but significantly higher number of larvae drifting from the woodland stretch than the open, even though they were equally distributed between the two areas.

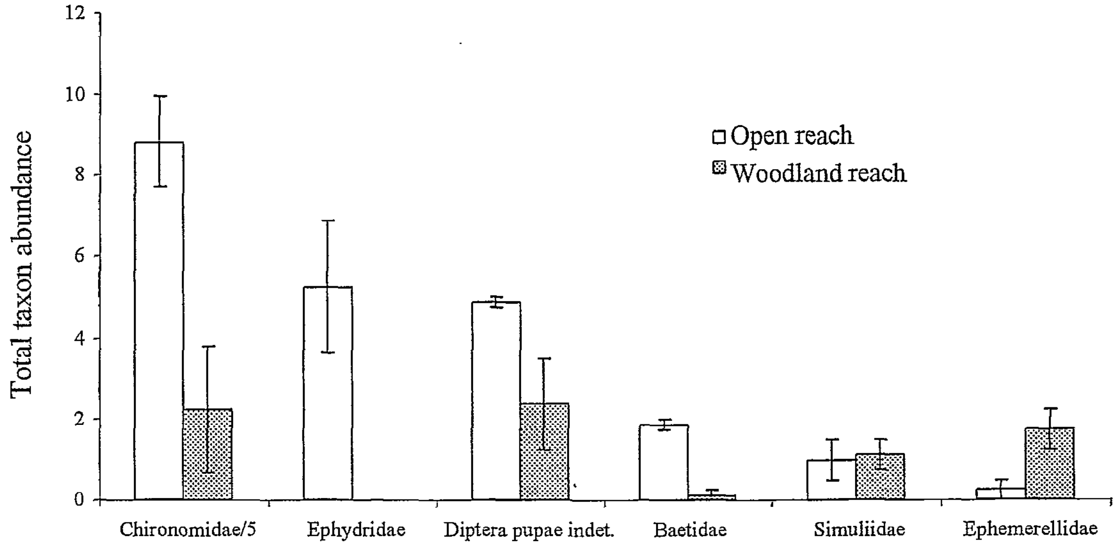


Figure 6.6. Results of drift trap samples taken on two occasions (May and June 1998) in 'wood' and 'open' regimes, four traps per regime. Mean ± 1 S.E.

6.4 Discussion

This work has demonstrated the importance of specific types of habitat not only for aquatic larvae but also for the terrestrial adults. Changes to the riparian landscape have potentially important consequences for invertebrate abundance and diversity in streams via their effect on terrestrial adults. Work on *Agapetus fuscipes* (Chapter 5) and latterly on many other terrestrial insects has shown that insect species often require different habitats for the different stages of their life-history. Thus it is possible that the abundance of a particular habitat may not be as important as its proximity to other, different, habitats.

> 'Management should not see the landscape elements in isolation. An approach that considers the relationships between separate landscape elements is crucial'.
> (Samways & Steytler, 1995)

The results generated by the malaise traps suggest that many adult caddis distribute widely. In general terms it appeared that most species had no association with a particular habitat but scattered with no significant preference between trees and open areas (e.g. Hydroptilidae). The reality is likely to be much more complex than this, with diversity of taxa and distribution being a function of all the available habitats. Sweep samples from 1996 suggested that Hydroptilidae for instance show strong negative-association with very open areas, especially in the first half of the year. The spring and autumn months are primary periods of emergence for aquatic insects (Williams & Hynes, 1976, in Gore, 1985) and so patterns like this may represent a seasonal component, with subsequent redistribution of adults to other areas. Several species however were particularly distinct and consistent in their site of capture by malaise traps. The most obvious of these was *Beraea maurus*, which was only ever found in woodland. Others included *Sericostoma personatum* (found near trees and in the open – very rarely in woodland), *Glyphotaelius pellucidus* (found in woodland), plus *Limnephilus extricatus*, *Limnephilus lunatus*, *Drusus annulatus* and *Potamophylax* sp. (all near trees). Obvious preferences aside however, the fact that virtually all the caddis were found, at some point, in each of the three habitats suggests a large amount of movement between the contrasting vegetation types. As the traps were operational for approximately five days at a time, it is likely that this movement was diel in nature. This is supported by evidence from sweep samples, taken in 1998. It must be considered though that insects may have been actively attracted to malaise traps, particularly in more open environments, biasing results towards higher than usual abundance in these areas.

It would seem that habitat diversity is not only important in order to accommodate a range of different species, but also necessary for individual species. This was evident when sweep samples were taken (summer 1998) and patterns of distribution were analysed over 24-hour periods. Several families, for example Psychodidae, Chironomidae and Culicidae, together with species such as *Drusus* and *Agapetus*, showed strong diel variation in their distribution between woodland and open areas. Samples collected from the grazed field also revealed significant abundances of adult invertebrates at various times of day (Culicidae, Chironomidae and *Agapetus*). A male and female *Ischnura elegans* (a damselfly) were also collected from the grazed vegetation after dark. The grazed section was also the only one with a notable amount of exposed marginal macrophyte (*Apium*) – a factor which was recorded as the most important environmental variable for most Odonata (Samways & Steytler, 1995). A grazed regime adjacent to a fenced or wooded area may then provide a suitable habitat for many odonate species, as these authors also list shade as an important requisite for this group of insects.

Similarities between 'open' and 'wood 'sticky-trap samples were partially explained once it was confirmed that many adult insects flew between stretches on a daily basis, rather than confined themselves to one particular habitat throughout their lives. The distribution of Psychodidae showed no overall difference between woodland and open over a period of several weeks, yet Psychodidae demonstrated a very obvious affinity for woodland at certain times of the day. It is likely that persistently low 'background levels' of some adults, in all areas, may have obscured peak abundances in specific areas at specific times of day. This is certainly likely with larger caddis such as *Potamophylax* (Limnephilidae), which was recorded on sticky-traps in low numbers in both the woodland and the open. Clearly this caddis used both woodland and open stretches of habitat, the former for refuge, the latter perhaps for oviposition. It is also likely that this behaviour is not unique to this caddis. Consequently, despite the relatively distinct appearance of riparian stretches such as woodland or grazed fields, regimes such as these are highly unlikely to function independently of each other for many invertebrate species and families.

The clear difference in distribution shown by Sialidae caught on sticky-traps however demonstrates that some insects may not require the intimate juxtaposition of different stretches. Adult sialid abundance was heavily concentrated in the open stretch, and at times was extremely localised within this area. Over the course of this project the larvae were found almost exclusively in similar ungrazed (fenced) sections. Elliott (1977) states than Sialidae pupate in damp soil or vegetable debris in the middle of clumps of sedge, and in addition he reports that *Sialis* eggs are usually laid on the stems and leaves of plants overhanging the water. These conditions (sedges and overhanging vegetation) were often only present, in an abundance that gave them meaningful ecological significance, in ungrazed open sections. Bankside vegetation of any kind, including sedges, is often sparse in stretches of woodland suggesting again that Sialidae would prefer ungrazed open stretches.

One question raised by the work with *Agapetus* in 1997 was that of conflict between adult and larval survival. If this is indeed the case then the requirement for different habitat at different life-history stages has the potential to affect mortality rate in the stage least able to re-locate to a suitable environment. Drift has been found to be the predominant mechanism of invertebrate movement within stream communities (Townsend & Hildrew, 1976, in Gore, 1985). Previous work had demonstrated a dramatic decline in the abundance of larval *Agapetus* following recruitment in woodland stretches - a decline that could be due either to mortality, or departure via drift. The use of drift-traps was therefore expected to clarify this. Unfortunately a *Ranunculus* cut in July reduced water levels thereafter to a point where the drift-traps could not function properly. An increase in total drift from woodland (over that seen in the 'open') was noted in May, although the numbers concerned were too low to suggest this was a significant result. More work on this aspect of invertebrate ecology in tandem with adult distribution could show whether drift is used as a measure to counteract adult migration upstream (Hynes, 1970, in Gore 1985) or if it is a mechanism to avoid predation or sub-optimum conditions (Gore 1977, in Gore 1985).

Water levels did not however affect the ability to take Surber samples, which showed no difference in the abundance of *Agapetus* larvae between the two stretches overall. Similarly, the sticky-traps showed no overall difference in the abundance of *Agapetus* adults between the two stretches. It is interesting to note however that 'woodland adult', 'open larvae' and 'open adult' populations all appeared to oscillate in synchrony, with an increase in populations in June followed by a large decrease in August, and a subsequent rise again in September. This was not a pattern demonstrated by 'woodland larvae', which appeared to present a much more stable population, without fluctuation. Although such patterns represent a large degree of interpolation of the available data (and it would be speculative to comment further without the benefit of many more sampling occasions or instar-analysis of the caddis) it could be tentatively suggested that these patterns may represent univoltine and bivoltine regimes, in response to the particular habitats. Benthic samples also revealed large differences in the abundance of other taxa between the wooded and open sections. Several caddis families, mayflies and some diptera all demonstrated overall preferences for one regime over the other (Figure 6.5).

Despite the often unique combinations of distribution shown by the adults and larvae of individual taxa during these experiments, it is clear that habitat diversity both within and adjacent to the watercourse is paramount. This is true, for instance, not just to cater for the diverse requirements of the different families within a group (e.g. mayflies) but also for different species within a single genus (e.g. *Baetis*) (pers. comm. Dr. P. Armitage). The same is also true of other large families such as the *Simuliidae* (Bass, 1998), and *Culicidae* (Cranston *et al.*, 1987) whose larval and adult habitats are extremely varied. A study to identify the relative importance of particular types of riparian vegetation to specific adult insects (particularly those that are rare or uncommon) would thus be valuable to explain inter- and intra-family variations. This would be of particular importance where a landscape prone to change abuts the watercourse, such as farmland.

It is probable that many taxa are non-specific in their habitat requirements as adults, and will adapt to a newly changed regime - where a previously grazed section is fenced for instance. Many species however have highly precise habitat needs. One form of active management would require the species-specific connection to be made between insects and their requisite habitats, in order to identify areas requiring preservation or enhancement. Ormerod *et al.* (1990, in Samways & Steytler, 1995) found for example that 10 metres width of bankside strip between forest plantation and stream was insufficient to attract the dragonfly *Cordulegaster boltonii*. Samways & Steytler (1995) themselves suggest that certain other Odonata species require at least 20 metres width of bankside strip. An undertaking on this level for every species would, though, be exceedingly complex. In reality, management for habitat diversity (maximum heterogeneity) alone should be sufficient to ensure taxonomic diversity - producing 'a linear matrix where each species would be able to find it's niche' (Drake, 1995).

6.5 Summary

- Samples of caddis caught during summer 1997, by malaise traps placed in wooded, near-trees and open regimes, showed that caddis taxa have different preferences for various types of vegetation. Examples of both specific habitat requirement, and broad-range use of various habitats were shown.

- Samples of both adult and larval invertebrates were taken from a single section of stream between May and September 1998. The stream section consisted of two contrasting areas of management, 'wood' and 'open', which were both sampled. Samples were taken passively and actively from bankside herbs and trees (sticky-traps and sweep-net samples respectively), from the stream benthos (surber samples) and from the water column (drift traps).

- The combination of these experiments provided details of the use to which various riparian zones were put by aquatic invertebrates and their terrestrial adults. Integration of the results from each set of experiments was not intended to provide a species-by-species analysis of habitat requirement at each life-stage, but a preliminary assessment of the importance of different vegetation regimes.

- The total abundance of adult insects caught in the two regimes ('wood' and 'open') was not significantly different for any of the four sampling occasions over the summer period. The total diversity of adult insects caught, however, was significantly higher in the 'open' stretch in May and September (but not in June or August).

- For the most part, long-term differences in the abundances of individual adult taxa were not significantly different between the woodland and open stretches. However, short-term studies conducted over two 24-hour periods revealed a variety of adult behavioural patterns in response to the woodland and open sections.

- The three habitats, woodland, open (tall herbs) and open (grazed field) were all important (to greater or lesser extents, depending on the specific taxa) in the dispersal of adult invertebrates.

- The importance of a particular habitat, such as a grazed field, to adult invertebrates may not be immediately obvious. The extreme mobility of these adults compared to their larvae means that even regular monitoring may miss a transitory visit to a certain area. On an individual stream basis, identification of bankside areas that may play separate roles in adult invertebrate distribution is therefore essential. Maintenance of these distinct areas of diverse vegetation structure also must be a paramount objective. Together with contrasting management regimes, such as woodland, herbaceous strips and short grazed sward, this includes the need to enhance or provide structurally different plants within the stretches.

7. DISTRIBUTION OF *Gammarus Pulex* & THE BULLHEAD *Cottus Gobio* WITH RESPECT TO MARGINAL VEGETATION

7.1 Introduction

Freshwater shrimps, *Gammarus pulex*, are among the most abundant invertebrates in chalk streams and account for a high proportion of the total invertebrate biomass. They are able to tolerate a wide range of environmental conditions, and are associated with many different kinds of habitat. They are also omnivorous and thus able to exploit many different kinds of food. Not only are they are major processors of plant detritus in streams (thus providing a quantitatively important link between trophic levels) but they are also voracious predators and can, potentially, strongly influence other invertebrate populations. *Gammarus* are also an important food item of many fish, particularly benthic feeding species. Bullheads can be the most abundant fish in chalk streams, in terms of numbers and biomass. Not only are they important predators of benthic invertebrates, they are a favoured food item of brown trout. They thus act as an important trophic link between food levels, as do *Gammarus*.

Gammarus pulex and the bullhead may therefore be highly important species in terms of trophic functioning and animal biomass. Despite their importance, relatively little is known about either their habitat use or interactions. Both species can be found in abundance in main channel gravel, *Ranunculus* and vegetated margins. Neither showed any strong preference for any one habitat for much of the year, in the first year's investigation, although *Gammarus* appeared to prefer gravel in January. Bullheads are said to prefer gravel habitats, where they hide under large stones during the day. However, many were found in margins and *Ranunculus* during this study.

One of the many functions of margins may be to provide invertebrates with refugia from predators. Many of the larger, predatory invertebrate species (e.g. damselfly larvae, true bugs and beetles) are found in the vegetated margins. This may not only be related to their foraging ecology but also to the need to escape predatory fish, which tend to favour large-bodied active species. *Gammarus* are particularly active and are also one of the larger species of invertebrates, when fully grown. They may therefore potentially use the margins as refugia from fish, particularly benthic feeders such as bullheads.

Predator-prey relationships in lakes have been shown to be stabilised by the presence of spatial refugia for zooplankton, such as macrophyte beds. These refugia prevent fish from consuming all the available prey, thus preventing large oscillations in both fish and zooplankton populations. This also stabilises zooplankton–phytoplankton interactions and prevents lakes becoming dominated by phytoplankton over time. One of the dominant features of chalk streams is both the high abundance and diversity of fish and invertebrates, but also the stability of populations of both groups. Hydraulic factors are undoubtedly responsible for much of this stability, but the high abundance of marginal vegetation may play a role, by 'buffering' the interactions between fish and invertebrates.

This investigation concerns the interaction between *Gammarus pulex* and bullhead, and the role marginal vegetation plays in this interaction.

7.2 Methods

7.2.1 Stream Sites

Two streams were selected for intensive experimental investigation:

- The upper reach of the Bere stream at Roke cress farm provided one suitable site, due to its stable, spring-fed flow and shallow, uniform stream profile (Plate 7.1). It was also safe from human disturbance and accessible.
- The other site was located at the abandoned FBA site at Waterston manor, near Puddletown, where a small tributary of the Piddle flowed from old cress beds. At this site, flow was less than in the Bere stream, such that there were distinct areas of deep (>5cm) and shallow (<5cm) water, in a longitudinal fashion, as the stream flowed toward the Piddle.

At both sites, there were abundant *Gammarus* and bullheads, together with extensive marginal vegetation. This comprised principally of *Apium* (Fool's water-cress) and water-cress, *Rorippa nasturtium-aquaticum*.

Plate 7.1: The Bere stream, just above Roke Farm, showing the main stretch used for the extensive *Gammarus* and Bullhead enclosure/exclosure experiments described below. Summer 1997.

7.2.2 Experiments

Experiments were carried out in August 1997 and January 1998.

A) Quantitative investigation of the distribution and abundance of *Gammarus* and bullhead in main bed gravel, *Ranunculus* and Margins. Bere stream. (August 1997)

Gammarus and bullheads were sampled using standard Surber samplers. This method allowed both animals to be accurately sampled using the same method, in each habitat. Animals were preserved in alcohol in the field and sorted and identified in the laboratory. They were also assigned to size classes.

B) Investigation of factors involved in *Gammarus* distribution. Bere stream. (August 1997)

Experimental cages were used to investigate three factors potentially involved in the distribution of *Gammarus*. These were a) flow regime b) substrate preference c) bullhead predation

Cages (measuring 20 x 20 x 10cm) were constructed from tough plastic 5mm-pore mesh. A clean, unglazed quarry tile was introduced into the bottom of each cage to prevent it being swept away by the current and to prevent organisms escaping through the mesh bottom when the cage was removed from the water. Three different types of substrate were introduced into the cage, on top of the tile:

1. washed gravel of uniform size
2. cut and washed stems of *Apium* and cress (a fixed number per cage)
3. strips of green plastic tarpaulin (cut to structurally mimic plant stems and leaves whilst providing no food value)

Cages were placed in two habitats – either in mid-stream in the main flow or in the vegetated margins, out of the flow. A single large bullhead was introduced into half of the cages, which were then sealed. The following treatments were thus established: (in-cage substrate/position in stream/fish regime)

Gravel / Margin With Fish	Gravel / Margin No Fish	Gravel / Middle With Fish	Gravel / Middle No Fish
Plastic / Margin With Fish	Plastic / Margin No Fish	Plastic / Middle With Fish	Plastic / Middle No Fish
Apium / Margin With Fish	Apium / Margin No Fish	Apium / Middle With Fish	Apium / Middle No Fish

Each treatment had four independent replicates. Cages were introduced into the stream and collected 10 days later. Invertebrates that had colonised the cages were collected, preserved in alcohol and sorted and identified in the laboratory.

C) Quantitative investigation of the distribution and abundance of *Gammarus* and bullhead in main bed gravel, *Ranunculus* and Margins. Bere stream. (February 1998)

The quantitative survey of *Gammarus* and bullhead undertaken in August 1997 (section A above) was repeated in February 1998.

D) Investigation of factors involved in *Gammarus* distribution. Bere stream. (Jan. 1998)

The experiment designed to examine the distribution of *Gammarus* (section B above) was repeated in January 1998.

E) Quantitative investigation of the distribution and abundance of *Gammarus* in deep and shallow main bed gravel and margins. Waterston stream. (August 1997)

The distribution of *Gammarus* in shallow (<5cm) and deep (>5cm) areas of Waterston stream (gravel and margins) was investigated quantitatively using similar methods to that used in the Bere stream (section B above). The same small cages were introduced into distinctly different depth areas in the stream, with the same types of substrata in the cages as before. No bullheads were put in any of the cages, as this experiment was designed to focus on other factors.

F) Experimental investigation into the distribution of *Gammarus* and Bullhead in shallow and deep areas. Waterston stream. (August 1997)

Artificial substrata (clean, unglazed quarry tiles) were introduce into the stream in August 1997. They were placed on the bed gravel in shallow and deep areas, across a range of flow conditions. Invertebrates and fish were sampled 10 days later by placing a Surber net over the tile and sweeping all organisms from under and around tiles into the net. Organisms were preserved in the field in alcohol and sorted and identified in the laboratory.

G) Experimental investigation into the effect of bullheads on *Gammarus* distribution. Waterston stream. (August 1997)

Experimental cages (the same dimensions and construction as in section B above) were placed in deep and shallow areas of main channel gravel. Each cage had a large tile as ballast and a layer of uniform, washed gravel overlying the tile. Cages were placed in deep and shallow areas. A single large bullhead was introduced into half of all cages, creating four treatments: Shallow/Fish, Shallow/No fish, Deep/Fish, Deep/No fish. Cages were left to colonise with invertebrates for 10 days, then harvested in a similar manner as above. Each treatment had four replicates.

H) Experimental investigation into habitat preference of *Gammarus* across deep and shallow areas. Waterston stream. (August 1997)

Open-sided cages were introduced into deep and shallow areas. Cages had two types of substratum – either clean, washed *Apium* stems or clean, washed gravel. Cages were harvested after 10 days in a manner similar to section G above.

7.3 Results

The following is a summary of results, and follows the same format as Section 7.2 (methods). No statistical analysis is included.

A) Quantitative investigation of the distribution and abundance of *Gammarus* and bullhead in main bed gravel, *Ranunculus* and Margins. Bere stream. (August 1997)

The distribution and abundance of the size classes of bullheads and *Gammarus* is shown in Figure 7.1 (top panel - distribution of bullheads, lower panel - distribution of *Gammarus*). The majority of bullheads are found in gravel and *Ranunculus*. There is some evidence of a shift in habitat from gravel to *Ranunculus* as bullheads grow. Very few fish are found in margins.

Small *Gammarus* are found largely in *Ranunculus* and *Apium* margins. Larger *Gammarus* are found predominantly in the margins. Very few *Gammarus* of any size are found in the gravel and only small individuals are found in *Ranunculus*.

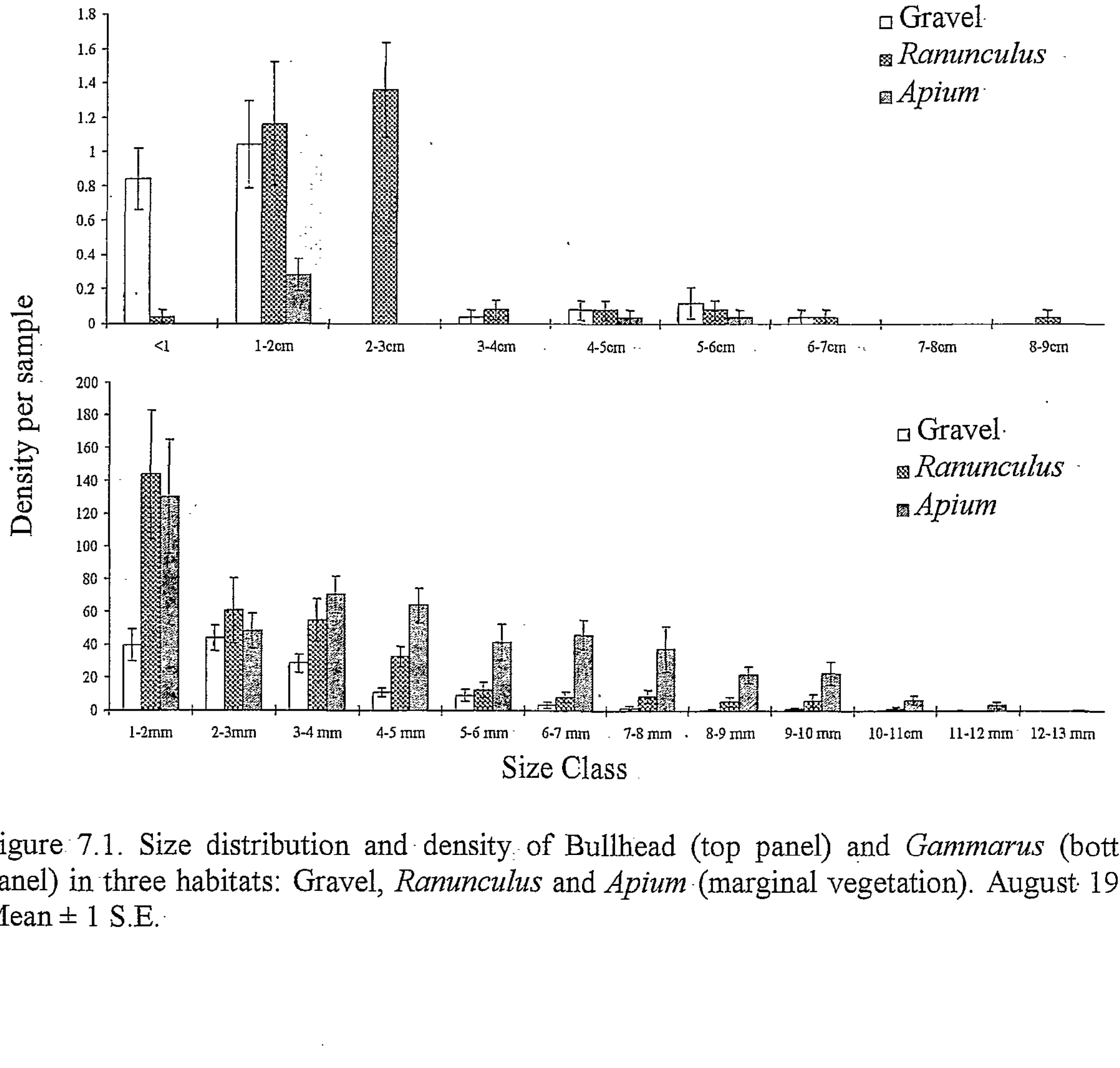


Figure 7.1. Size distribution and density of Bullhead (top panel) and *Gammarus* (bottom panel) in three habitats: Gravel, *Ranunculus* and *Apium* (marginal vegetation). August 1997. Mean ± 1 S.E.

B) Investigation of factors involved in *Gammarus* distribution. Bere stream. (August 1997)

The distribution and abundance of *Gammarus* across the 12 treatments is shown in Figure 7.2 (page 101) top panels. Large *Gammarus* in particular are found more abundantly in cages without fish. More *Gammarus* of all sizes were found in the middle compared to margins. Although substrate appeared to have little effect with fish, *Gammarus* preferred gravel in the absence of fish. Thus, in the absence of fish more *Gammarus* are found in cages in the middle channel containing gravel – the habitat where they were rarest in investigations of the natural habitat.

C) Quantitative investigation of the distribution and abundance of *Gammarus* and bullhead in main bed gravel, *Ranunculus* and Margins. Bere stream. (February 1998)

In direct contrast to the distribution of bullheads in summer, winter distribution shows most fish now in the margins, particularly the 4-5cm size class (Fig. 7.3, top panel). Similarly, in contrast to the distribution in summer, *Gammarus* are now found in greatest abundance in the gravel, compared to either *Ranunculus* or margins (Fig. 7.3, bottom panel). There thus appears to have been a switch in the distributions of both *Gammarus* and bullheads, from summer to winter.

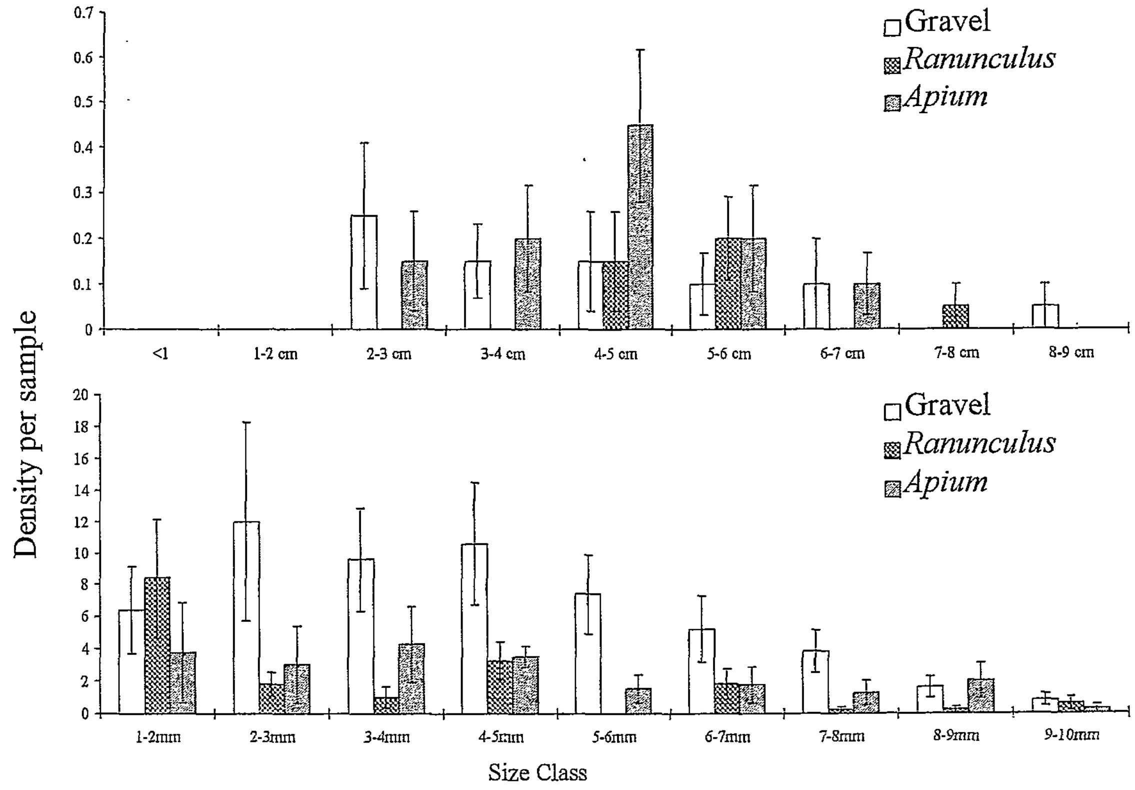
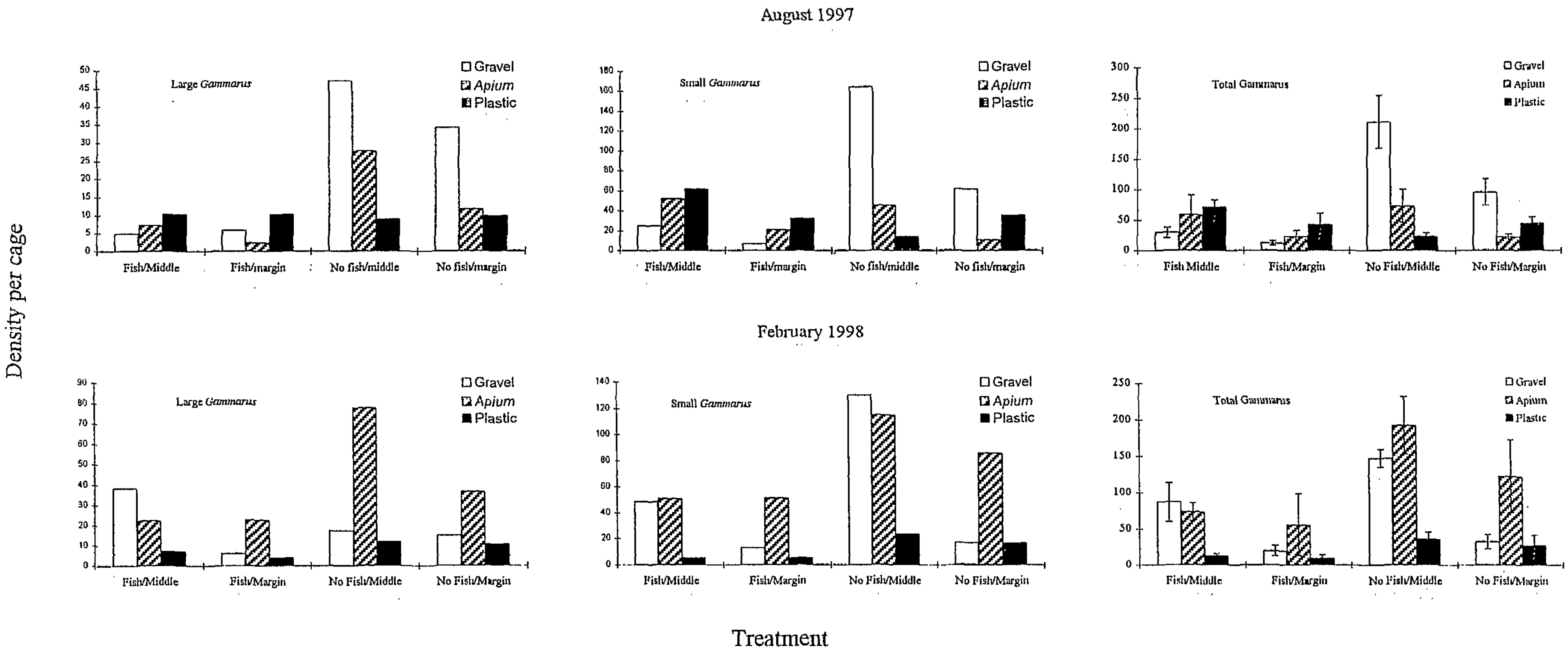


Figure 7.3. Size distribution and density of Bullhead (top panel) and *Gammarus* (bottom panel) in three habitats: Gravel, *Ranunculus* and *Apium* (marginal vegetation). February 1998. Mean ± 1 S.E.

Figure 7.2: Density of *Gammarus* in experimental cages with three treatments: Cages either contained fish (one large Bullhead) or no fish (No Bullheads); Cages were placed in either the middle of the stream (Middle) or in the vegetated margins (Margins); Cages contained either gravel, *Apium* stems or plastic strips. Mean ± 1 S.E.



D) Investigation of factors involved in the distribution of *Gammarus*. Bere stream. (February 1998)

The distribution and abundance of *Gammarus* across the 12 treatments is shown in Fig. 7.2 (page 101) bottom panels. *Gammarus* are again found in greater abundance in fishless treatments and again more were found in cages placed in the middle of the stream. In winter, *Gammarus* (particularly large individuals) preferred *Apium* rather than gravel, in contrast to their summer distribution. Despite the switch in habitat selection from summer to winter, *Gammarus* still demonstrated a similar preference for fishless cages placed in the middle, although there appears to be a preference in winter for *Apium*, rather than gravel.

E) Quantitative investigation of the distribution and abundance of *Gammarus* in deep and shallow main bed gravel and margins. Waterston stream. (August 1997)

The distribution of the two size classes of *Gammarus* showed strong differences. A greater number of large *Gammarus* were found in shallow margins, compared to shallow gravel, although they were still abundant in the latter habitat (Fig. 7.4). Very many more large *Gammarus* were found in the shallow gravel compared to deep gravel. Large *Gammarus* were almost absent from this habitat, whereas smaller *Gammarus* showed little difference between shallow and deep gravel.

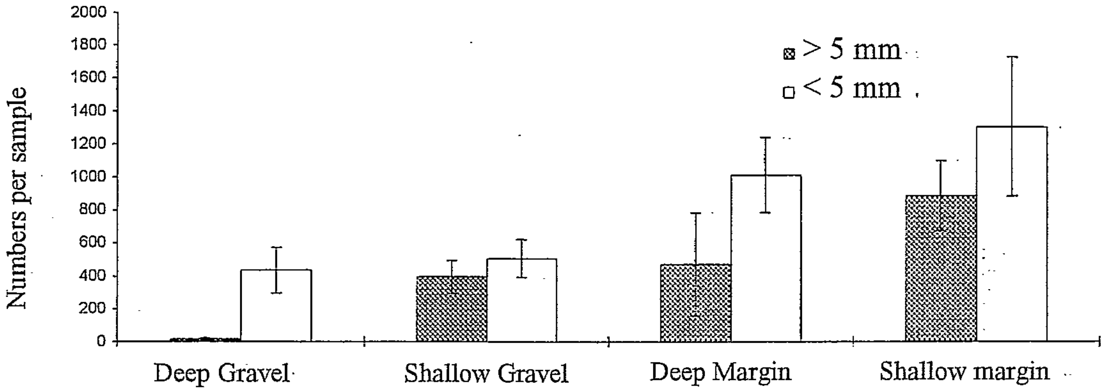


Figure 7.4. Distribution of large (>5mm) and small (<5mm) *Gammarus* in shallow and deep gravel and margins. Waterston stream, August 1997. Mean ± 1 S.E.

F) Experimental investigation into the distribution of *Gammarus* and Bullhead in shallow and deep areas. Waterston stream. (August 1997)

Tiles and invertebrates were placed into depth classes: 0.5-3cm, 3.5-6cm, 6.5-10cm and 10cm+ (Fig. 7.5). There were two patterns of distribution seen in invertebrates and fish. *Gammarus* were abundant under shallow tiles but numbers declined dramatically under tiles at a depth greater than 6cm. Bullheads were rare under shallow tiles but increasingly more abundant under deeper tiles. Mayflies, chiefly *Ephemerella ignita*, were rarer under deeper tiles. *Asellus aquaticus* were more common under deeper tiles.

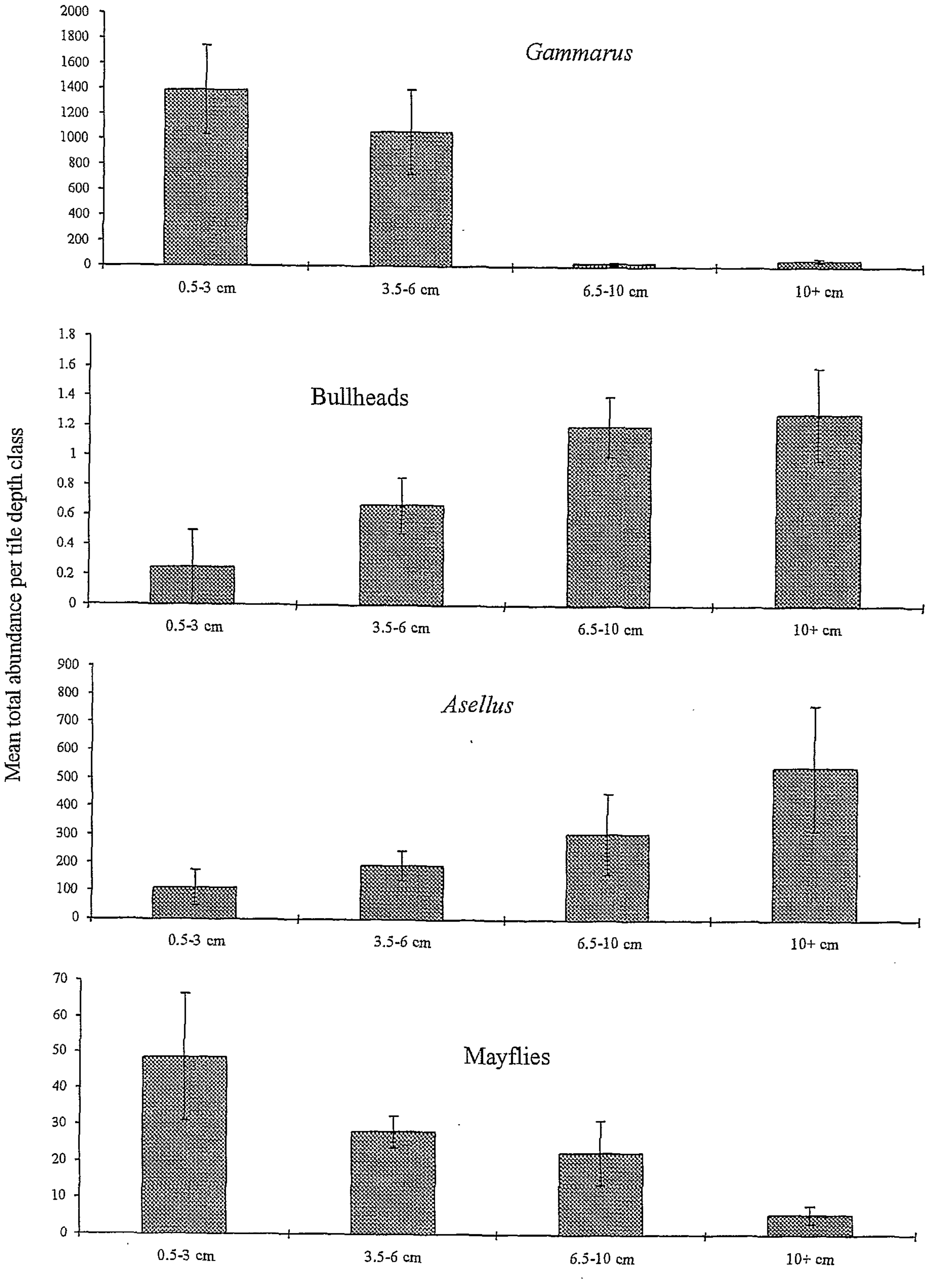


Figure 7.5. Distribution of invertebrates and Bullhead fish under tiles placed at different depths. Waterston stream, August 1997. Mean ± 1 S.E.

G) The effect of bullheads on *Gammarus* distribution. Waterston stream. (August 1997)

The distribution of *Gammarus* in shallow gravel is strongly reduced in cages with fish added (Fig. 7.6, top panel). Very few *Gammarus* were found in cages placed in deep gravel, either with or without fish.

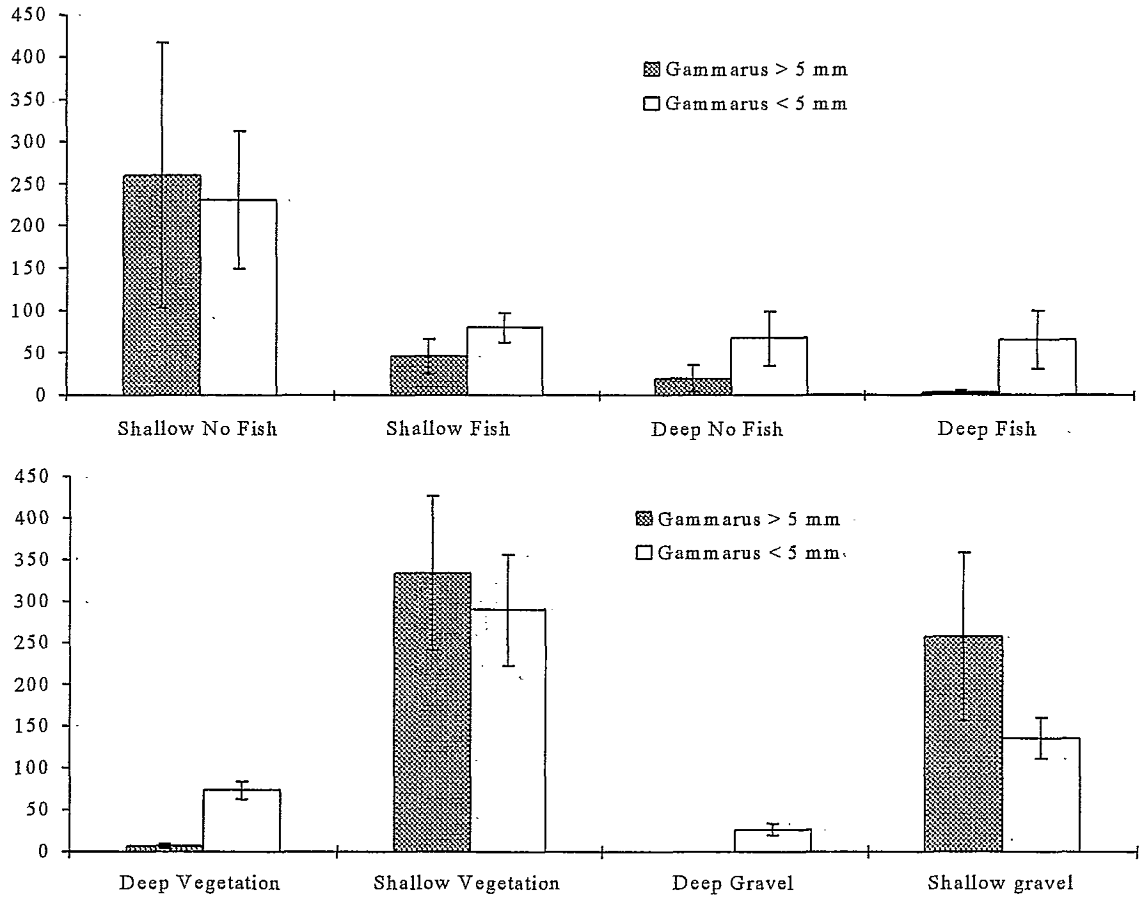


Figure 7.6. Top panel - Density of *Gammarus* in experimental cages with two treatments: Fish (containing one large Bullhead) and No Fish (no Bullheads). Cages were placed in shallow and deep water on gravel. Waterston Stream, August 1997. Mean ± 1 S.E. Bottom panel – Density of *Gammarus* in open-sided cages with two treatments: Vegetation (containing *Apium* stems) and gravel. Cages were placed in shallow and deep water on gravel. Waterston Stream, August 1997. Mean ± 1 S.E.

H) Habitat preference of *Gammarus* across deep and shallow areas. Waterston stream. (August 1997)

In shallow water, *Gammarus* preferred cages with *Apium* in them, rather than gravel, but this effect was more marked in small individuals (Fig. 7.6, bottom panel). Large *Gammarus* showed little obvious preference. Very few *Gammarus* were found in cages of either type (*Apium* or gravel contents) placed in deep water areas.

7.4 Discussion

The experiments into *Gammarus*–bullhead interactions have demonstrated a number of important aspects. The results of the Bere cage experiments demonstrated that *Gammarus* preferred habitats without fish in both summer and winter. The middle of the stream was also preferred to the margins on both occasions. Fish predation would thus appear to be a dominant factor in *Gammarus* distribution.

The distribution of *Gammarus* in natural habitats in the Bere stream showed that large individuals in particular were found mainly in vegetated margins, in summer. In winter, there was a strong shift in habitat with most *Gammarus* (particularly large individuals) being found in the mid-channel gravel, rather than in the margins. Physical conditions changed in the stream from summer to winter, with the depth increasing markedly, from approx. 15 cm to approx. 30cm. The water velocity also increased. Margins were, however, almost as abundant in winter as summer, with vegetation width ranging from 30 – 100cm on each bank, in both seasons.

The habitat shift between summer and winter by *Gammarus* was not therefore in response to either low flows or to marginal vegetation reduction. It is however consistent with fish predation or fish avoidance. Bullheads were rare in margins in summer, but abundant in the mid-channel gravel and Ranunculus. Margins would thus have been a relatively 'fish-free' area during summer. In winter, however, bullheads were common in the margins - which would not therefore have provided *Gammarus* with such anti-predation protection as in summer. *Gammarus* may thus have chosen the habitat which they intrinsically favoured, given that both had high predation pressure. The cage experiments showed that *Gammarus* favoured the mid-stream habitat rather than the margins.

The results of the experiments in Waterston stream demonstrated that bullheads exerted a strong effect on *Gammarus* distribution, both across the stream, from mid-channel to marginal habitats, and longitudinally, from shallow to deep areas. Bullhead avoided shallow areas, presumably because of the risk of predation or stranding. *Gammarus*, on the other hand, strongly favoured shallow habitats. The results of the tile experiment demonstrated that *Gammarus* avoided deep tiles (where bullheads were common) and preferred shallow tiles (where bullheads were rare).

Gammarus and bullhead are both strong predators. The opposite responses of mayflies and *Asellus*, with the former avoiding deep areas and the latter avoiding shallow areas, may be responses to the two predators. Mayflies are highly favoured prey of bullhead during summer and may be excluded from habitats where bullheads are very common. *Asellus* are known to be preyed upon strongly by *Gammarus*, and they may thus avoid *Gammarus* in preference to bullheads.

The Waterston cage experiments showed that *Gammarus* preferred shallow gravel due to the absence of bullheads. *Gammarus* were rare in cages in the shallow gravel when bullheads were introduced. *Gammarus* were also rare in cages in deep areas, both with and without fish, but this can be attributed to the fact that these cages represented habitat 'islands' which *Gammarus* were unable to colonise effectively, due to the presence of bullheads in the gravel around them.

There was some indication that *Gammarus* preferred margins to gravel, even in the absence of bullheads, although the experiment with the open-sided cages showed that *Gammarus* were almost as abundant in cages with gravel as in cages with *Apium*. Again, few *Gammarus* colonised cages placed in the middle, as these probably acted as relatively inaccessible 'islands' where the risk of predation in the surrounding areas was too high.

The quantitative survey of *Gammarus* distribution in Waterston stream showed that large *Gammarus* were abundant in shallow gravel and in shallow margins. High numbers were found in deep margins, but they were almost absent from deep gravel. This indicated that margins provided a refugium for large *Gammarus* from bullheads, where these latter were common. Small *Gammarus* were common in deep gravel, however. These would have been less susceptible to bullhead predation, both because the fish preferred large *Gammarus*, and because interstitial areas in the gravel may have provided an adequate temporary refuge.

As a result of work on Perch (*Perca fluviatilis*) in pond enclosures, Diehl (1992) suggests that vegetation enhances both invertebrate biomass and species richness. In addition he reports that the negative effect of fish predation on invertebrates is delayed by submerged vegetation due to decreased foraging efficiency. In the chalk stream environment, vegetated margins provided *Gammarus* with refugia from bullhead predation. Whether *Gammarus* actively selected margins in the presence of bullhead, or their distribution is due to predation reducing numbers in mid-channel gravel, is unknown. The spatial separation of *Gammarus* from their major predator in summer may allow their population to remain at a high level all year round. Population pressure will presumably force many *Gammarus* individuals to disperse from optimal areas to areas where bullheads are common. In this manner bullheads may be ensured a constant source of food, dispersed from areas (margins or shallow areas) which they cannot exploit themselves. This would be expected to confer stability on both *Gammarus* and bullhead populations. A similar conclusion is reached by Diehl (1992) who states that feeding patterns [in benthivorous fish] may be stabilised by the presence of structural complexity. Given bullheads' conservation status (listed in Annex 2 of the Habitats Directive 92/42/EEC) it would be expected that factors which contribute to a stable population would be encouraged.

Margins may act as fish predation refugia for many other species of invertebrate. Trout are reluctant to forage in margins and so many invertebrate species that are favoured prey of trout may be expected to use margins as refugia. These experiments have demonstrated the functional importance of margins as refugia for invertebrates. Where marginal vegetation is rare or absent, invertebrates may be highly vulnerable to fish predation. As a consequence, the absence of high populations of reproducing individuals may then reduce the food 'supply' available to fish, thus reducing fish populations. Fish population instability may thus result from disruption of the tightly coupled interactions that exist between fish and invertebrate populations.

7.5 Summary

- One of the important functions of margins in streams may be to provide refugia for invertebrates such as *Gammarus* from fish such as bullhead. These two species are dominant species in chalk streams, and Bullhead have Conservation status under Annex 2 of the EU Habitats Directive.

- Experiments with artificial exclosures and substrata showed that fish presence/absence was the dominant factor in the distribution of *Gammarus* in the two streams investigated. In the absence of fish, *Gammarus* showed little preference for either vegetation or gravel as a microhabitat.

- In natural habitats in summer, *Gammarus* (particularly large individuals) was very much more abundant in margins and rare in gravel. Fish showed the opposite distribution, being common in gravel and rare in the margins, suggesting a strong negative correlation in the distribution of the two species.

- In winter, bullhead were found to be abundant in margins and somewhat less so in gravel. *Gammarus* showed the opposite distribution, being abundant in gravel and rarer in margins. This demonstrated a habitat shift by the two species, the distribution of bullhead possibly driving that of *Gammarus*.

- The spatial separation of the two strongly interacting species in summer (with *Gammarus* using the margins as a predation 'refuge') is likely to contribute to population stability for both species. This feature of margins – the buffering of fish/invertebrate interactions - may also have important implications for other species and contribute to high diversity and abundance of invertebrates in chalk streams, particularly for groups vulnerable to fish predation, such as large-bodied beetles, bugs and molluscs.

- Continuous stretches of marginal vegetation such as *Apium* should be permitted to grow in summer to provide refugia for invertebrates from fish predation. Removal of vegetation from one bank may mitigate against a resulting increase in water depth (should this be deemed undesirable), but complete removal of marginal vegetation should be avoided.

8. SEASONAL CHANGES IN MARGINAL HABITATS IN THE RIVER FROME

8.1 Introduction

One of the original aims of this project was to examine the functional dynamics of the bankside habitat in response to natural seasonal effects and different management regimes. This objective has been addressed in the preceding chapters of this report, however the relationship between seasonal succession of bankside vegetation and stream hydraulics at the bank/water interface was not examined. The original intention was to examine the link between seasonal changes in bankside vegetation and the formation and distribution of instream habitat but commitments to the main sampling programme prevented this aspect of the work being fully explored. However the arrival in January 1998 of an MSc student from Germany provided an opportunity to start a preliminary investigation of the bankside zone of a meander in the lower reaches of the River Frome. This work was continued after June partly by volunteers and later by casual labour.

The bankside habitat is a dynamic zone where large seasonal changes in physical appearance occur. Optimal management of this area to balance conservation issues with those of flood-control and other physical disturbances requires basic information on the year round functional aspects of this habitat. It is crucial to know the relative importance of time of year, bank profile and riparian characteristics in determining the faunal assemblages that inhabit this marginal zone

The main objectives of this study were to:

- carry out an **intensive survey** of seasonal variation in the faunal assemblages of bankside habitat,

- examine the observed changes with respect to bank profiles and riparian vegetation,

- analyse and identify the stability and sensitivity to change of physically different bank types.

This work is still in progress and the faunal data have not been analysed fully. The account below outlines the scope of the work and reports on progress.

8.2 The Study Area and Methods

8.2.1 The physical environment

A section of the River Frome at East Stoke was selected which exhibited a wide range of flow-types, bank profiles and riparian characteristics within a short reach. (about 250m). Twenty-three sites were chosen to represent examples of these (Figure 8.1).

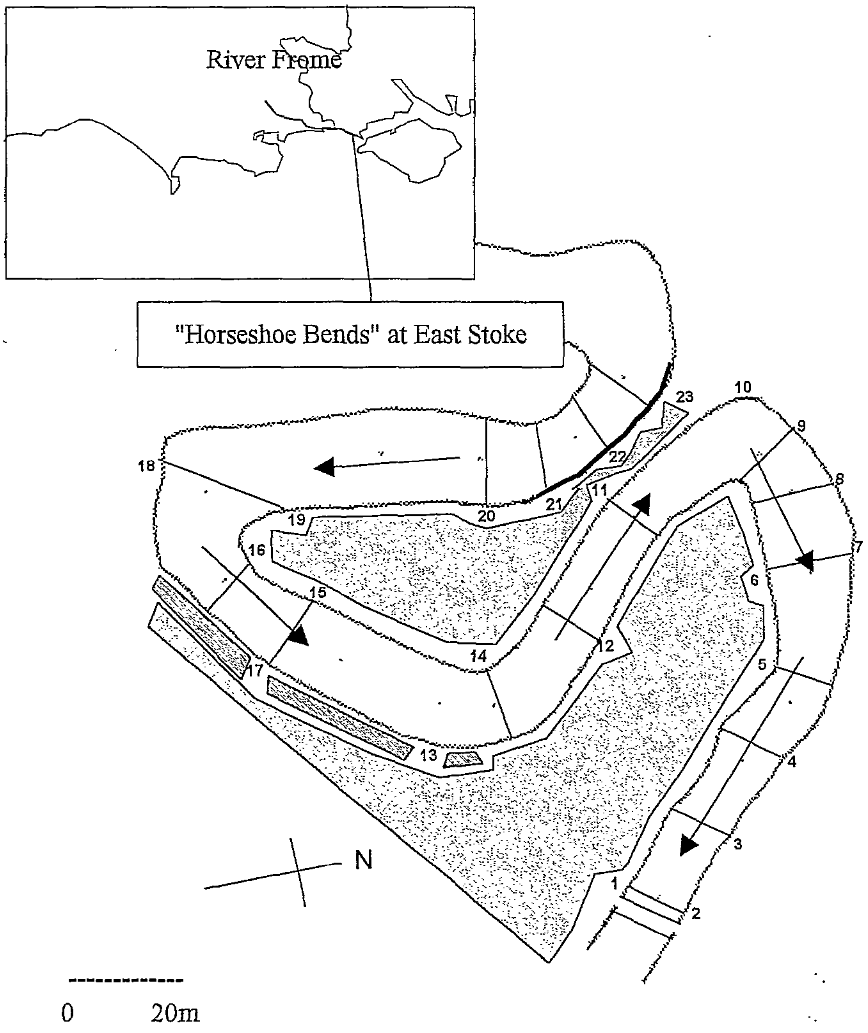


Figure 8.1 The location of the study area, sites and transects along the River Frome. Stippled areas represent ungrazed grassland. Wooded strips are indicated by hatched areas and the revetted section (iron pilings) is shown with a bold line.

Riparian features are shown in Plates 8.1 and 8.2. The reach comprises a large meander. Deep slow sections on the bends alternate with shallower glides and runs colonised by *Ranunculus*. The only riffle occurred between sites 6 and 7 and was most obvious in the summer during low flow periods. The selection of this reach has the added advantage that results obtained can be linked to another study examining mesohabitat distribution and faunal composition in the Frome.

The River Frome at this point is a moderate sized river with a mean daily flow between 5 and 10 cumecs. The channel has a mean width in the reach of 11.5 m and a mean depth of 0.68m (based on 17 transects). The maximum depth is 2.2 m. Cross-sections at 17 locations are shown in Figure 8.2.

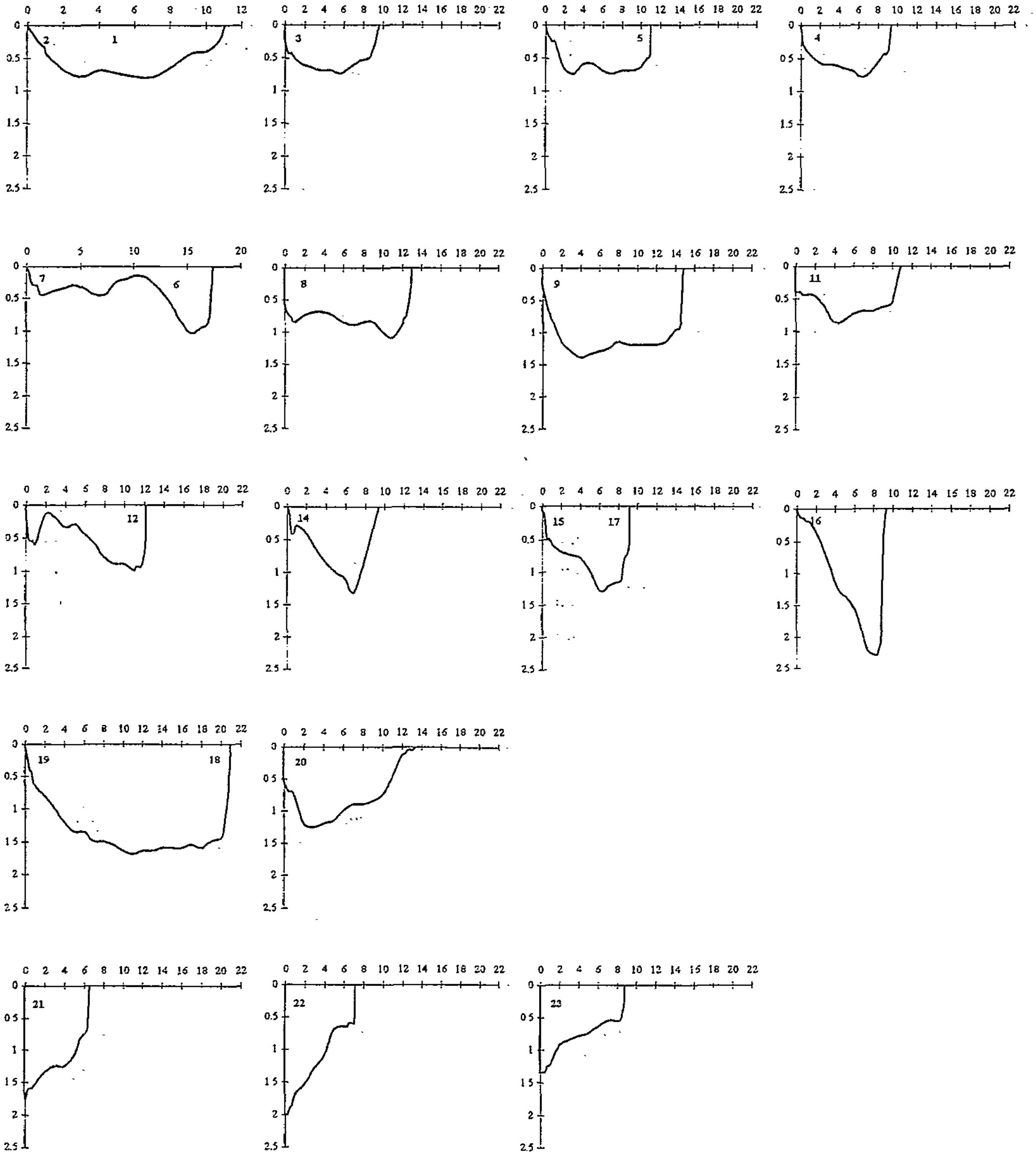


Figure 8.2. Cross-sectional areas at 17 locations in the study area. Additional information on the substratum and profile type of each site is shown in Table 8.1.

Table 8.1 Physical features of the 23 sites – U ungrazed, G grazed, W wooded, O open.

SITE	VELOCITY February	 June	 October	PROFILE Category	PROFILE Description	SUBSTRATUM Dominant	Riparian Features
1	0.12	0.09	0	1	Shallow no step	Sand	U/O
2	0.12	0.20	0	1	Shallow no step	Gravel	G/O
3	0.44	0.49	0	1	Shallow no step	Gravel+clay	G/O
4	0.72	0.33	0	1	Shallow no step	Gravel	G/O
5	0.58	0.50	0	3	Shallow step	Gravel	U/O
6	0.58	0.78	0.81	2	Steep no step	Gravel	U/O
7	0.40	0	0	1	Shallow no step	Gravel+earth	G/O
8	0.30	0.13	0	3	Shallow step	Clay	G/O
9	0.29	0.05	0	2	Steep no step	Gravel+clay	G/O
10	0.36	0.06	0	2	Steep no step	Clay	G/O
11	0.60	0.27	0	3	Shallow step	Gravel	U/O
12	0.14	0.29	0.17	3	Shallow step	Clay	U/O
13	0.07	0.18	0.11	4	Steep step	Clay	U/W
14	0.13	0.05	0	1	Shallow no step	Sand	U/O
15	0.28	0.11	0.07	1	Shallow no step	Sand+gravel	U/O
16	0.08	0.06	0	1	Shallow no step	Sand+gravel	U/O
17	0.46	0.05	0	3	Shallow step	Clay	U/W
18	0.06	0.05	0	2	Steep no step	Clay	G/O
19	0.21	0.05	0	1	Shallow no step	Clay	U/O
20	0.36	0.17	0.09	3	Shallow step	Clay	U/O
21	0.62	0.46	0.55	4	Steep step	Iron	U/O
22	0.64	0.60	0.54	4	Steep step	Iron	U/O
23	0.82	0.45	0.46	4	Steep step	Iron	U/O

Bank profiles of each site were considered to be a feature which would influence seasonal changes in faunal occupation of the marginal zone. There is a wide range of profile shapes and these have been categorised into 4 main types in Table 8.1, and are illustrated in Figure 8.3.

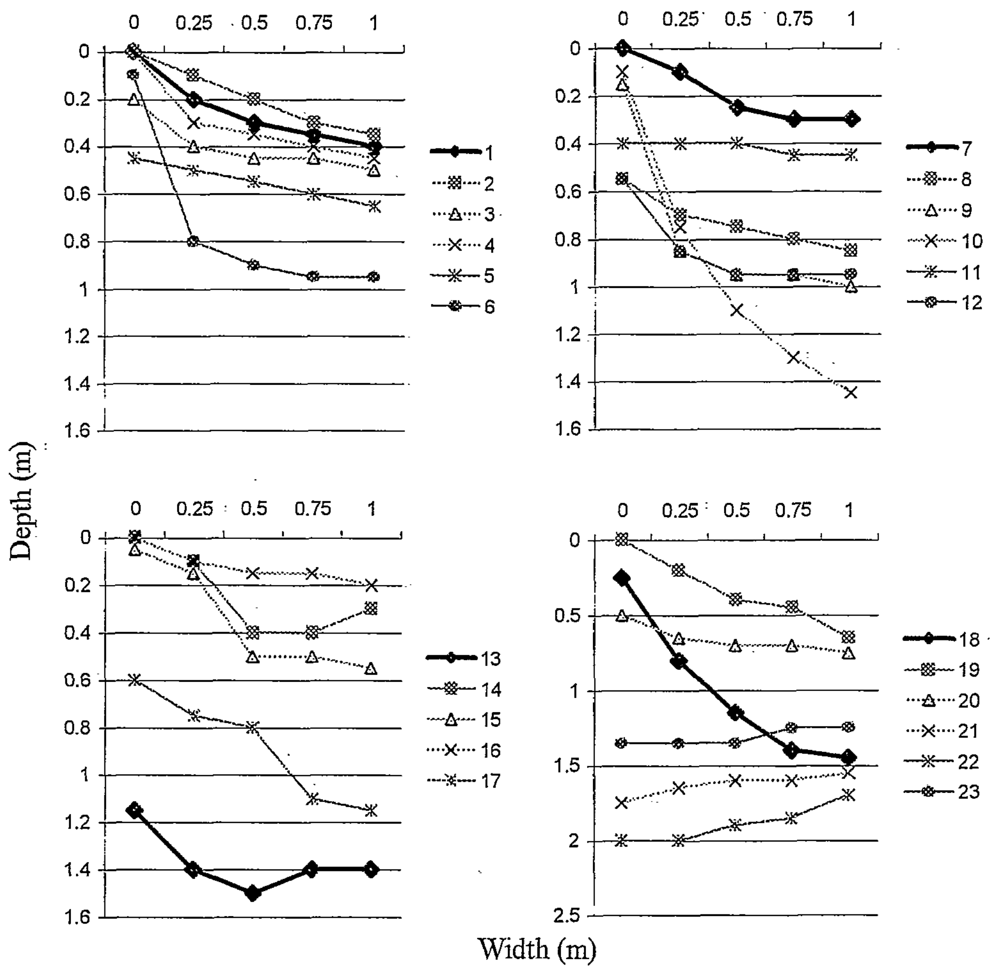


Figure 8.3 Bank profiles at the 23 sites.

Velocity measurements were taken at every site on all sampling occasions. The objective was to determine flows as close to the bank vegetation as possible to characterise current speeds in the boundary layer at the vegetation / water interface. Generally three replicate readings were taken at approximately 0.3m depth 0.3m from the bank. The distribution of velocities at each site between January and November 1998 is shown in Figure 8.4. It is clear that there is considerable variation in flow at all sites with ranges from about 1.2 m/s in the early part of the year to zero n the late summer. These changes may be very sudden following the snagging of drifting vegetation which can deflect flows away from the bank thereby reducing velocities at the site. Similarly growth of bankside vegetation above, below or at the site may result in similar wide fluctuations in water velocity.

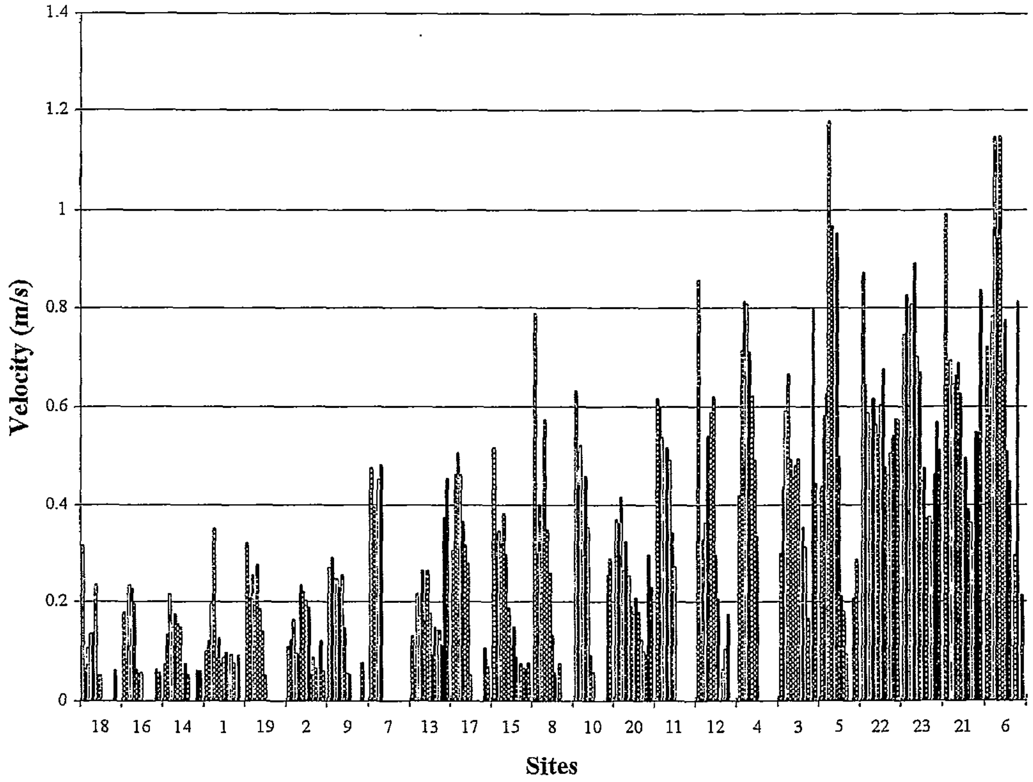


Figure 8.4 Seasonal changes in water velocity at each site over the period January to November 1998.

Each of the 23 sites was characterised by a specific habitat architecture with a dynamic vegetative component superimposed on the basic profile. However categorisation/ classification of these sites is difficult because conditions changed radically throughout the period of study. Despite this it was possible to recognise five basic types:

- *Glyceria* dominated 4,8,11
- *Phalaris* dominated 1,2,3,5,6,12
- Bare with occasional snags of vegetation 9,10,13,17
- Mixed *Glyceria/Phalaris* with occasional *Apium/Berula* stands 7,14,15,16,18,19,20
- Revetted banks - iron pilings with growths of moss 21,22,23

8.2.2 Faunal sampling

In order to meet the objectives of this study it was necessary to obtain samples of animals with an estimate of their relative abundance. The variable nature of the sites posed problems for sampling but a timed 15s sweep net technique provided a method that could be used at anytime of the year and in all locations (Wright *et al.* 1992). The net (900 µm mesh, 230x255 mm frame, 275mm bag depth) was swept through water at the bank/water interface (see Figure 8.5). The material was then put in polythene bags, fixed with 5% formaldehyde solution and later sorted and preserved in 70% alcohol. Most faunal groups were identified to species level where availability of keys and size allowed. Exceptions were Hydracarina, Oligochaeta, recorded as such, and some dipteran families which were recorded at family or genus level. Chironomidae were recorded as sub-families and tribes. Samples were taken at approximately 3-week intervals and velocity conditions and vegetation at the site were recorded at the same time.

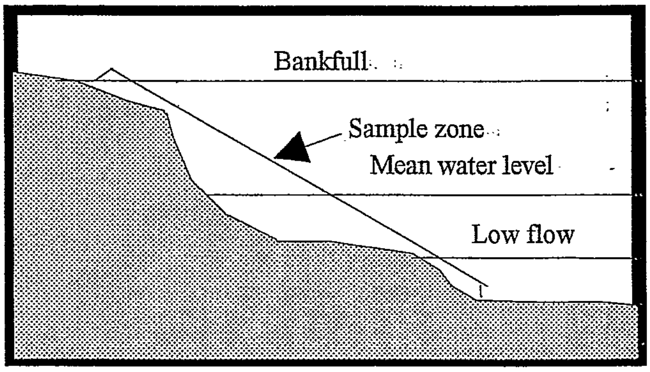


Figure 8.5 A schematic showing the extent of the bankside sampling zone

8.3 Results

To date only part of the data collected has been processed. Samples collected between January and the beginning of July have been identified but those collected in the second half of the year are still being examined. However to illustrate aspects of the work three sample occasions (February, June and October) have been analysed in more detail.

8.3.1 Total fauna

On the three sampling occasions together, approximately 170 taxa were found. This total will be altered in response to further identification and combinations of taxa but provides a good indication of the species richness of this habitat.

Table 8.2: The total number of taxa recorded at all sites in February, June, and October 1998

Groups	Feb	Jun	Oct
TRICLADIDA	5	4	5
MICROTURBELLARIA	0	2	0
GASTROPODA	7	7	13
LAMELLIBRANCHIATA	2	2	2
OLIGOCHAETA	1	1	1
HIRUDINEA	4	4	6
HYDRACARINA	1	1	1
CRUSTACEA	4	4	6
EPHEMEROPTERA	9	13	18
PLECOPTERA	0	2	3
ODONATA	1	2	4
HEMIPTERA	2	4	12
COLEOPTERA	9	11	23
MEGALOPTERA	1	1	1
TRICHOPTERA	19	23	22
DIPTERA	10	14	22
OTHER	0	0	1
TOTALS	75	95	140

The faunal richness increased by a factor of two between February and October (Table 8.2). The main contributors to faunal richness were Trichoptera, Diptera, Coleoptera, Ephemeroptera and Gastropoda. Total abundance also increased by a factor of two between February and October with Trichoptera dominating the winter samples and Trichoptera and Ephemeroptera the June samples. In October the fauna was characterised by high abundances of Diptera, Trichoptera, Crustacea, Oligochaeta and Gastropoda (Figure 8.6).

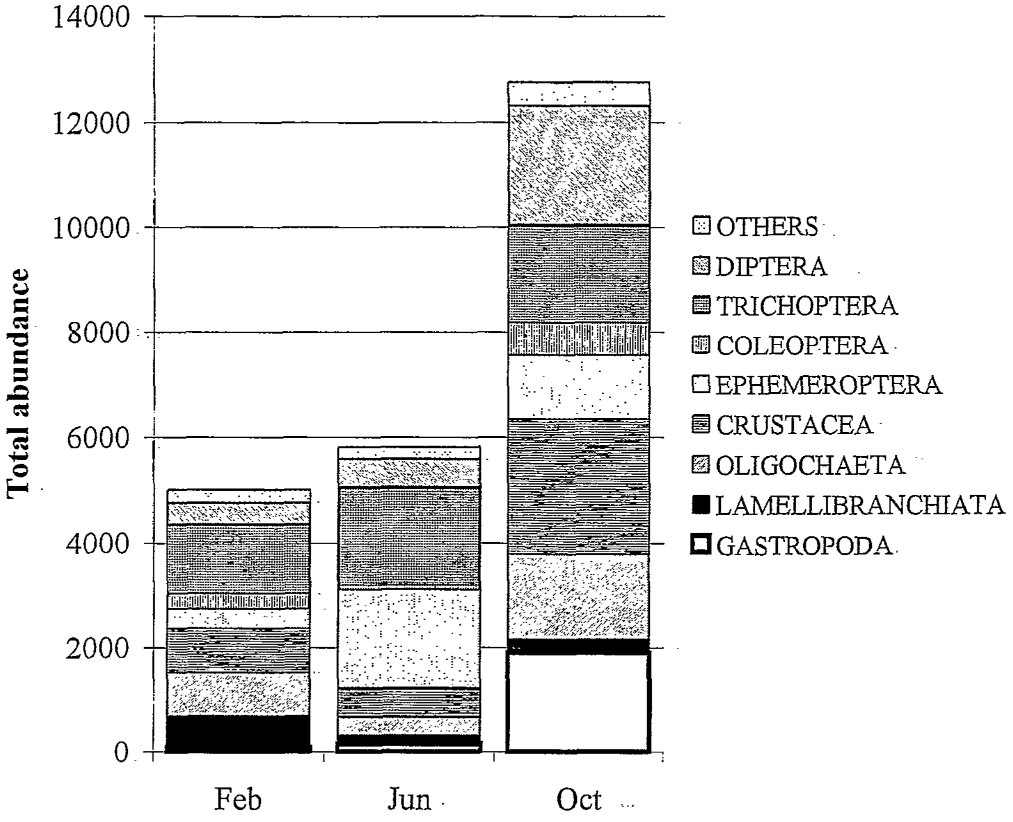


Figure 8.6 The faunal composition in three seasons based on collections from all sites.

Marked seasonal changes were observed between sites and Figure 8.7 illustrates the range of values for total taxa and abundance per sample at each of the 23 sites. These have been ordered according to the mean of the three months samples. There is a large range of values both within and between sites. It is hard to detect a pattern related to the physical features of the sites but the sites with the shallow profiles (for example 7,15,15,19) supported the highest mean number of taxa. The steeply-sloped sites and the revetted areas (10,13,21,22,23) supported fewer taxa. Abundance also showed great variability with consistently low numbers at the steep clay and earth bank sites (10,13) and high numbers in the shallow sloping sites (1,4,7,14).

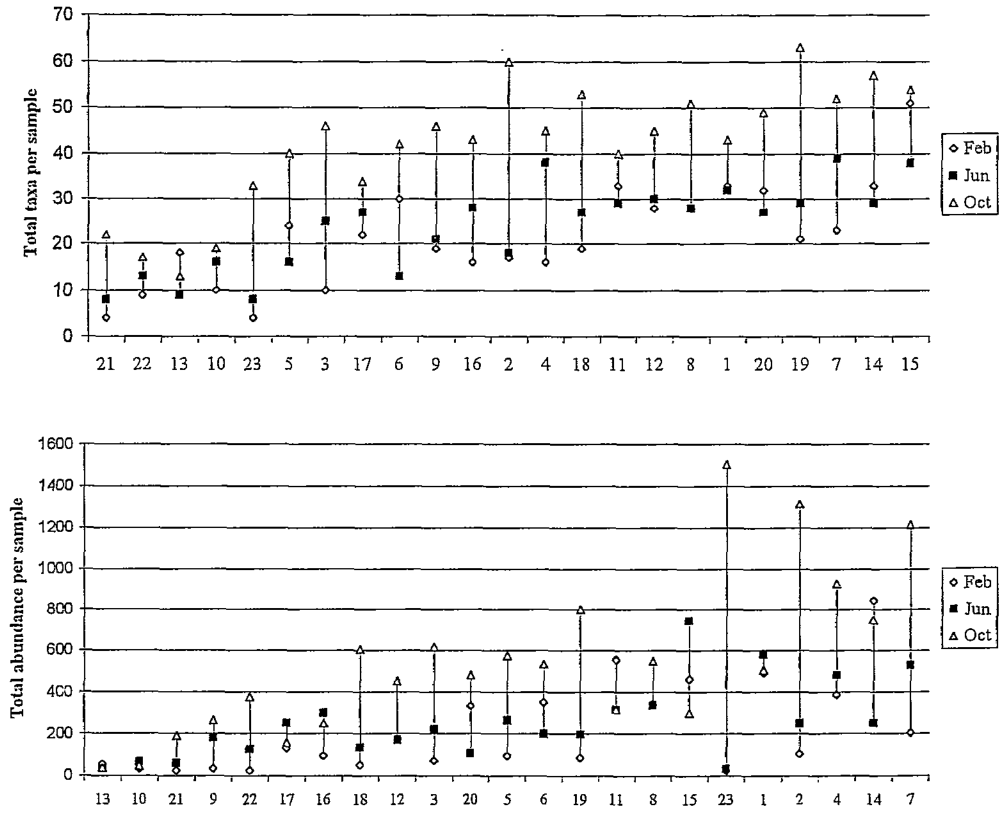


Figure 8.7 Seasonal variation in the number of taxa and abundance per sample in the 23 sites based on data collected in February, June and October.

8.3.2 Multivariate analysis

The fauna/site matrix was analysed using The family abundance data from the February, June and October sampling occasions were transformed using log(x+1) and the site/fauna matrix was analysed using CANOCO (Ter Braak, 1987) to examine the degree of association of samples from the 23 sites. The data were ordinated using Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980) which searches for major gradients in the faunal data irrespective of any environmental variables. The characteristics of the ordination are presented in Table 8.3.

Table 8.3. Ordination parameters for the DCA

Axes	1	2	3	4	Total inertia
Eigenvalues	0.324	0.236	0.092	0.075	2.552
Lengths of gradient	2.321	2.976	2.197	1.939	
Cumulative percentage variance of species data	12.7	21.9	25.6	28.5	
Sum of all unconstrained eigenvalues					2.552

Eigenvalues represent a measure of between-site variability and the eigenvalues of individual axes indicate their relative importance within the analysis (Verdonschot and Higler, 1989) with high values representing good separation of the sites. Thus Axis 1 is the most 'important' axis in this analysis and explains most of the variance in the data. Correlation of site axis scores with two environmental variables (velocity and profile category) shows a significant relationship only between Axis 2 scores and velocity (r = -0.737) and to a lesser extent profile (r = -0.557).

Figure 8.8. Presents the results of the DCA and clearly shows the over-riding seasonal component in the data. The three sample periods show little overlap indicating the existence of characteristic faunal assemblages in each of the three periods. There is a tendency for the high velocity sites to be found in the lower part of each season's cluster.

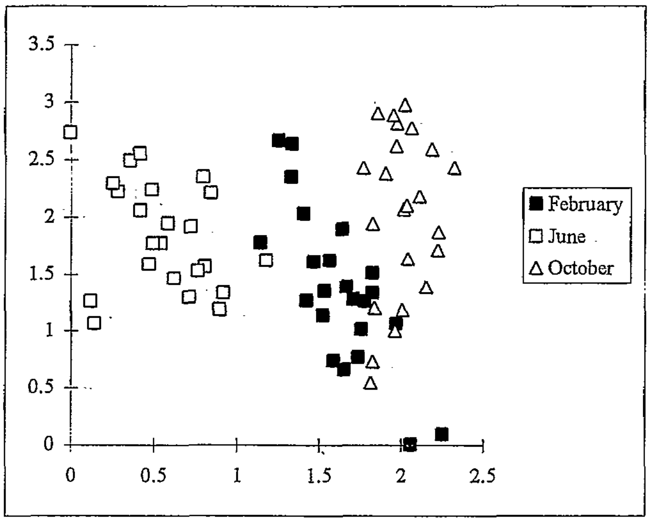


Figure 8.8. Ordination plot (Detrended Correspondence Analysis) of sample ordination scores of Axis 1 (X axis) and Axis 2 (Y axis) based on data from 23 sites in February, June and October.

The juxtaposition of sites within each seasonal cluster is illustrated in Figure 8.9.

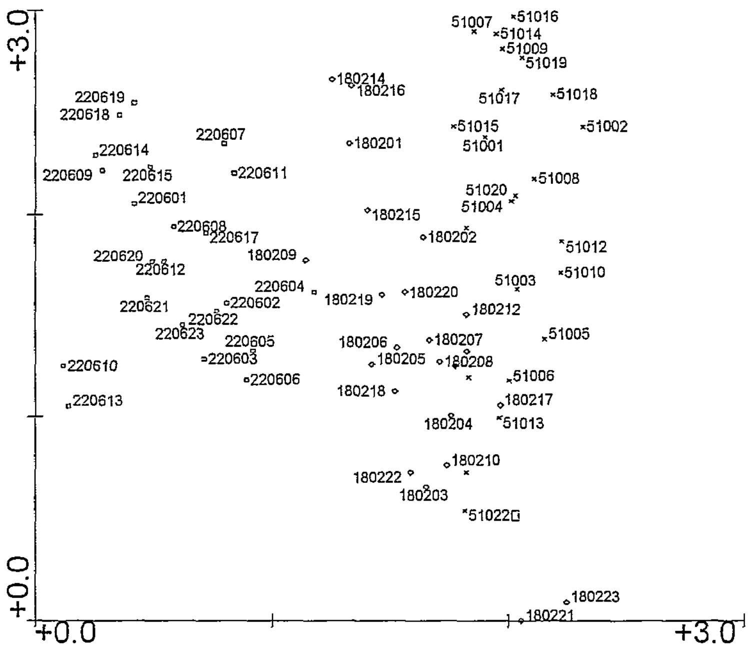


Figure 8.9. The juxtaposition of sites in the DCA ordination plot.

8.3.3 Seasonal distribution

When the full set of data are available for analysis it will be possible to examine changes in abundance over the whole year. As an illustration of the type of information which can be extracted, the distribution of selected species in the first half of the year is shown in Figures 8.10 and 8.11 for four contrasting sites comprising grazed open (3), ungrazed (open), shaded (17) and revetted (23).

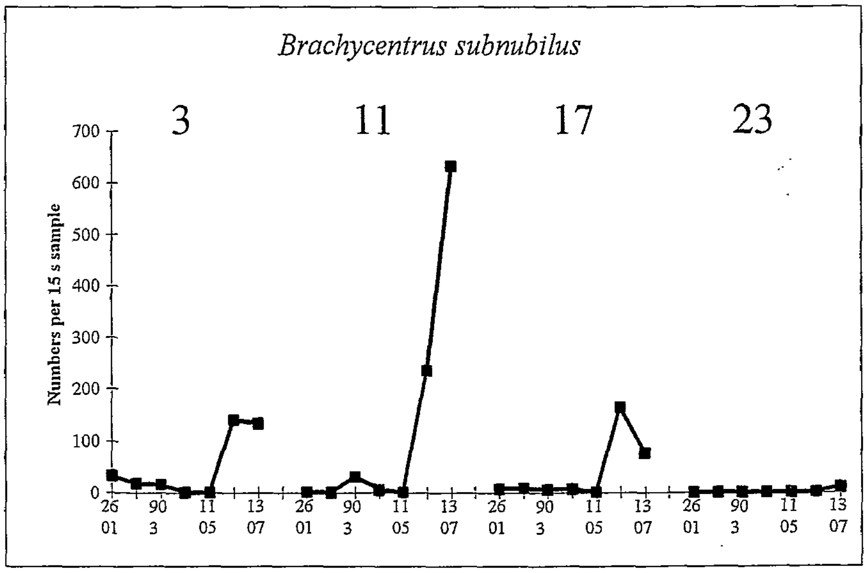


Figure 8.10. The distribution of *Brachycentrus subnubilus* at four sites 3,11,17, and 23 between January and July 1998

The caddis fly *Brachycentrus subnubilus* is a common and abundant species in the lower Frome. Final instar larvae overwinter and emergence takes place in the early spring. Figure 8.8 shows the relatively low numbers of late instar larvae in the winter where bankside habitat is not the favoured environment. However there is an increase in May when newly hatched instars are found in large numbers. The site 11 dominated by *Glyceria* supports the highest numbers of this species at this time. In contrast, *B. subnubilus* is almost absent from the revetted site 23 with moss on iron pilings.

In the second example, fluctuations in the numbers of three species of mayfly in the genus *Baetis* are illustrated (Figure 8.9). All sites support moderate-sized populations of these species but again, for one, *B. buceratus*, the open ungrazed site 11 dominated by *Glyceria* supports the highest densities in the winter months. Later in June, *Baetis scambus* reaches very high numbers at this site. Baetis *rhodani* shows little change between the four sites

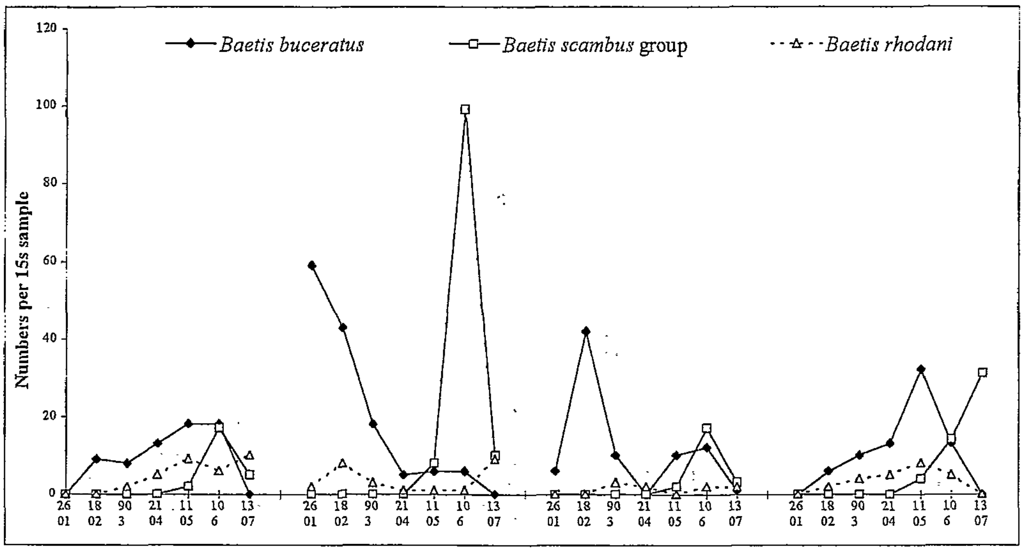


Figure 8.11 The distribution of 3 species of Baetis at four sites, (3,11,17 & 23) in the period January to July 1998

The seasonal changes in total abundance and number of taxa per site are shown in Figure 8.12. May 11th appears to mark the start of an increase in abundance at all but the revetted site. The number of taxa per sample increase gradually at all sites except Site 11 where after June there is a decline. Further data from the second half of the year will show whether these are continuing trends.

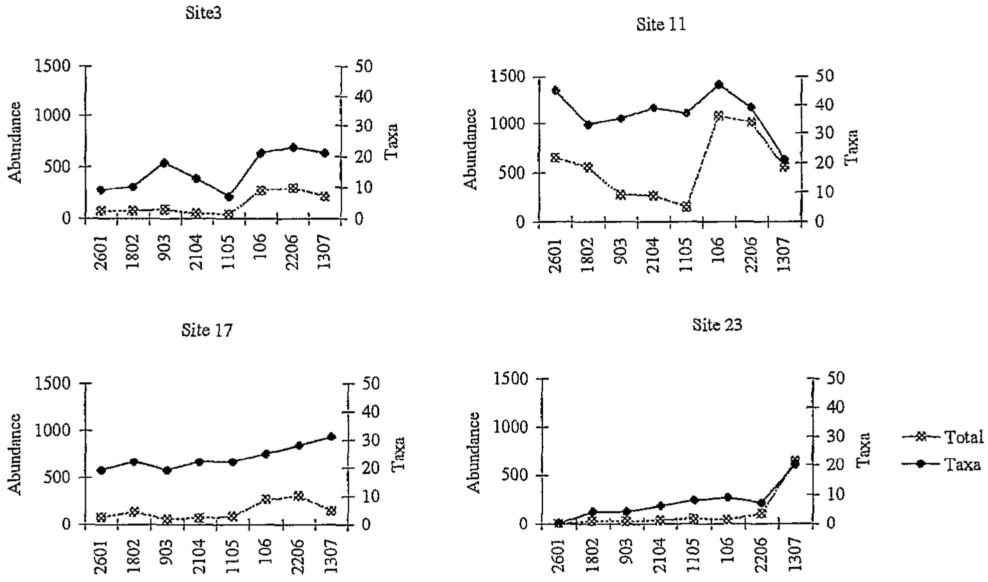


Figure 8.12. Seasonal changes in abundance and number of taxa per sample at four sites (3,11,17,and 23) over the period January to July 1998

8.4 Discussion & Conclusions

The bankside zone of moderate sized rivers poses several problems for the investigator. Replication of samples is difficult because the sites are generally so variable in their morphology. The seasonal shift in water level means that essentially different areas are surveyed on each sampling occasion. In this study we are examining this habitat at a meso- rather than a micro- scale and we include within the definition of bankside, the understanding that it is a dynamic environment. Another type of study might be interested in the specific changes that occur at one site. However since the bankside has been so little studied we considered that a more generalised approach would provide the most information at this stage. Thus we selected a range of sites but within this selection there are sites showing similar physical features (at least, based on their profiles) which could be considered replicates.

Preliminary results show that the bankside zone is a highly dynamic environment with individual sites experiencing a very broad range of conditions. The early part of the year up to May is characterised by relatively little change in total abundance, with a few noted exceptions such as Simuliidae and *Brachycentrus subnubilus,* which emerge early. Most "activity" would appear to take place in the second half of the year and October values for abundance and richness are the most extreme. An illustration of the variability of the environment is provided by the three sites situated on the iron pilings of the revetted section. The sites were close together and the substratum of each was exactly the same and covered by a dense growth of moss, so one might expect that they would support similar faunal densities. However the October abundances at site 23 were six times greater than at the other two sites, 21 and 22, mainly due to high abundances of oligochaetes, *Gammarus pulex* and Orthocladiinae larvae. An explanation will have to await further analysis but there may well be a random element following egg-laying and dispersal of first instar larvae. The direction of water currents carrying juveniles will fluctuate possibly resulting in settlement over a wide range of sites.

The data on the distribution of individual species will when all the analysis is complete provide information which can be used to optimise environmental management. If a specific bank type is proved to support particular species in high abundances then the river manager could avoid disturbance to this area. Similarly in order to maintain a high diversity along the bank, knowledge of the association of bank type with specific faunal assemblages is a necessary prerequisite.

This account summarises the state of the study so far. Samples will continue to be collected until the end of February and processing will continue for three months. We hope to have some information on life-histories of some of the main taxa and a complete record of velocity fluctuations over the whole year. It is too early to draw any firm conclusions from this work since as pointed out above, the most active part of the year appears to be after June. However there are indications that certain types of site are more favourable than others for maintaining both abundance and faunal richness and that a site which is suitable at one time of the year may be unsuitable at another. At the end of the 12-month study we hope to be able to quantify these findings in more detail.

9. MANAGEMENT IMPLICATIONS

9. 1 Background

Stream and river management has, in the past, typically addressed problems such as flood relief, recreational conflicts and water quality. Accordingly, much of the existing literature deals with the effects, on instream habitats, of engineering modifications like bank reprofiling, the addition of deflectors and weirs, and substrate replacement. In addition, wildlife enhancement often comes some way down the list of reasons for river management, whose other considerations include improvement of land drainage, maintenance of conditions suitable for navigation and improved geomorphic stability (RSPB, NRA & RSNC, 1994). It is also the case that bankside vegetation in the form of tall herbs, scrub and trees, whilst having conservation value, is often secondary to the need for flood prevention and is considered as a hindrance to bank access.

Marginal vegetation is nevertheless recognised as highly important for wildlife in general. Many specialised plants and animals occur only in the marginal zone, and it has also been observed as the last suitable refuge for fauna and flora once commonplace throughout the floodplain environment (RSPB, NRA & RSNC, 1994). It is possible in this respect to denote merit or worth to almost every type of riparian margin in terms of particular organisms: grazed regimes for beetles, adult dragonflies and fish-fry, tall herbs for small mammals and wild flowers, and woodland for native trees and bird life, for example. However, this says nothing about the 'value' of one management regime in comparison to others, or of the consequences of changing the land-use along a particular stretch of river. This project has shown that different land-management and land-uses in the areas adjacent to streams can have considerable implications for the invertebrate fauna within those streams.

9.2 Management definitions

A point to note is the definition of terms that have been used in this report, most notably the definition of 'grazed'. Drake (1995) refers to 'lightly cattle-trampled margins' and offers the tentative conclusion that they act as a superior habitat to fenced margins, suggesting also that half of rivers' lengths should be devoted to a lightly grazed regime. (Evidence of light trampling substantiated by the fact that just one of his sampling points were damaged by cattle). Most of the banksides sampled as 'grazed' for this project could arbitrarily then be defined as severely grazed, or overgrazed, as in most cases poaching sometimes running the entire length of field sections had occurred. As a result the streams were generally wider, much more silty, and slower flowing than non-grazed sections. Extensive foraging by dairy herds had left the banksides with mono-specific, cropped grass-swards, and direct pollution by the cows into the watercourses was evident. Heavy grazing such as this is described as 'poor' management practice by Ward *et al.* (1998). Similarly, this project would not recommend that large lengths of watercourses be grazed in this fashion, but would instead place a contradictory emphasis on either much more lightly grazed regimes, or ungrazed and woodland banks as areas of preferred conservation.

It must therefore be considered that disagreement or confusion over the value of grazed sections could arise as a result of misinterpreting the definition of 'grazed'. It is acknowledged that sections of river to which cattle are allowed access in moderate numbers may be useful to the river as a whole, as this would help provide a diverse linear mosaic of habitats which would maximise invertebrate taxonomic variety. One potential method to resolve the problem of definition could examine the effect of various livestocking regimes in combination with known coefficients for the amount of vegetation removed by various ages of different stock (LSU coefficients, RSPB, EN & ITE, 1997). Livestock unit coefficients show for example that one beef cow is considered equivalent to eight sheep, and measurements derived from such coefficients are used to determine if available grassland will meet fodder requirements. It may also be straightforward to assess how many days it will take, at a specified density of named animal, to damage bankside vegetation enough to cause knock-on effects to the invertebrate populations. In a comparative manner therefore, a consensus could be reached on definitions for terms like light-grazing and harmful-grazing, with the borderline point also clearly defined.

Confusion with the terms 'ungrazed/fenced' and 'woodland' or 'wooded' is less likely. Where fencing has been erected, floristic successional changes are much more prone to following a set-pattern. Anthropogenic influences in such sections are generally very low (unlike grazed areas) and thus the basic features of ungrazed and woodland areas are similar from site to site.

9.3 The impact of riparian management

This study has shown that the nature of the terrestrial bankside environment clearly influenced the abundance of invertebrates in streams, although only certain families showed significant differences. The groups that were notably rarer in grazed stretches, relative to ungrazed, were caddis, caenid and heptageniid mayflies, elmid beetles and the damselfly *Calopteryx splendens*. Invertebrate diversity was greater in ungrazed stretches with abundant marginal vegetation. These differences may well be related both to differences in the abundance of macrophytes across stretches and to differences in the abundance and reproduction of adult aquatic insects. Some groups more abundant in grazed reaches, particularly true bugs and some snails, may have favoured the silty, shallow 'pondlets' found at the margins of reaches running through grazed fields. These margins were also favoured by small fish, mainly minnows and sticklebacks. The other group of invertebrates that was found more abundantly in grazed reaches was the leeches (Erpobdellidae and Glossiphoniidae).

It might be expected that cattle which are allowed access to streams and rivers over dry summer periods may generally have a less harmful effect than those which are permitted to graze during spring and autumn, when the ground is much wetter. However, it is likely that a 'wet' summer may result in cattle placing less demand on rivers and streams for water, allowing marginal and instream vegetation to grow, and juvenile trout to encroach. For aquatic invertebrates, heavy grazing of aquatic plants in summer tramples both animals and habitat, and reduces the sites available for oviposition. Reduction of stock numbers would seem to be the main route of mitigation against such damage, such that 'light-grazing' were employed rather than 'severe grazing'.

Comparing woodland to ungrazed stretches, most invertebrate groups were less abundant in woodland. The overall abundance was generally lower in woodland habitats. The lack of *Ranunculus* in woodland will further depress abundance, particularly since high numbers of *Simulium* spp. and baetid mayflies favour this habitat. However, some taxa were much more abundant in woodland than in the other regimes that were studied, particularly the caddis larva *Agapetus fuscipes* and elmid riffle beetles. Elmid beetles may have needed the particular soil conditions found in woodland to pupate. This may be a critical life-stage for the beetles, without which they may be rare in habitats otherwise suitable for them. The management of banks for pupating beetles has received scant attention in the past. Preliminary observations and discussions suggest that many if not all aquatic beetles pupate on the bank. They are unlikely to favour the unstable, silty, excessively wet or desiccated soils that are typical of the margins of streams where cattle graze. Well-structured, stable, porous soils with firm root structure are likely to provide beetles with a stable, humid and undisturbed site for pupation. These type of habitats are more likely to be found on banks with a well-developed vegetation structure, including trees. Determination of beetle pupation sites represents an important area of future investigation. The high numbers of adult insects found in woodland terrestrial habitats indicates a different aspect of the woodland environment which may be vital for many invertebrates – that of oviposition. This is discussed in greater detail in section 9.4.

In the light of this information, best management of bankside habitats would seem to be to discourage heavy grazing along the banks of streams and rivers. This would prove advantageous to most invertebrate taxa in the stream and disadvantageous to only a very few. However, small fish such as minnows, together with some common bugs and snails, favoured the shallow, poached margins of grazed areas in preference to the marginal habitats of ungrazed or woodland areas. Poached margins do appear therefore to have some 'merit'. In reality therefore, fenced and wooded areas interspersed with stretches of lightly grazed field would be acceptable and even recommended in order to achieve maximum diversity of invertebrate and fish populations.

9.4 Adult (emergent) invertebrates & woodland

Patches of woodland were found to be of definite benefit to streams, even though these habitats were generally less productive. Reduced light levels under the tree canopies decreases both the productivity of macrophytes and algae, and hence the availability of refuge-areas and food for many invertebrates. Other studies have demonstrated the adverse impact of channel shading on fish populations due to the reduction of instream macrophyte cover (Swales, 1982, in Mason *et al.*, 1984) and suggest that overshadowing trees be removed (Roland Campbell, The Tweed Foundation, pers. comm.). Beneficially though, wooded areas can stabilise and strengthen stream banks, moderate stream temperatures, reduce sediment inputs, and provide important sources of organic matter (Osbourne & Kovacic, 1993).

Woodland areas may also provide a favoured habitat for many adult insects that lay their eggs in or near woodland, as was found to be the case with *Agapetus fuscipes*. Wooded areas then potentially act as 'sources' of drifting early instars of many species that colonise reaches below them, via oviposition at these sites. In any case, the presence of adults in woodlands indicates that this is a favoured habitat, without which they would presumably suffer greater mortality or have lower reproductive success. Meehan *et al.* (1977, in Mason *et al*, 1984) has shown that many emerging aquatic insects are actually dependent on this type of vegetation for completion of their life-cycles. It is unlikely though that many (or indeed any) adults spend their time exclusively in this environment, but rather use it, for example, as shelter when conditions in other habitats become less than favourable. The hot, dry conditions typical of open, grazed fields in summer may be strongly avoided by adults in order to reduce the risk of desiccation.

The large amount of movement both into and out of woodland, by different taxa, at different times of day, demonstrated the complex value of woodland stretches in combination with more open stretches nearby. It is likely therefore that part of the value of woodland to adult invertebrates is in its proximity to different neighbouring habitats. Thus it could be concluded that best management practice would encourage a patchwork of distinct riparian regimes, with blocks of woodland (perhaps no greater than 30 or 40 metres in length) adjacent to open areas, with a clear interface between the two. This diversity of habitat would certainly assist in achieving diversity of aquatic larvae, and cater for the habitat preferences and behavioural patterns in the great majority of emergent adults.

Thus, understanding how vegetation 'works' with respect to invertebrate life-histories can enable managers to prescribe best practices for banksides. In practice this is reasonably simple to achieve, compared to more intractable problems of abstraction or flow management. Simply fencing streams from stock will ameliorate streams for invertebrates and for fish, such as trout. (Where financial considerations prevent 'post and rail' fencing being erected, electric-fencing could be employed subject to the realisation that allowing cattle to re-access the stretch at a later date may be as harmful as not fencing in the first place). However, few invertebrates would suffer from a policy of fencing, although poached grazed margins may support semi-aquatic species not studied during this investigation. This would allow trees to grow naturally, and planting may also be encouraged - willows and alders are cheap and robust species to establish. Where streams exceed a certain size, flood risk would perhaps need to be assessed to ensure that excessive vegetation on the banks does not impede floodwaters. Trees, however, will eventually shade out marginal vegetation, producing a 'cleaner' more open stream channel.

9.5 The function of aquatic margins

Vegetated margins are functionally extremely important for chalk stream invertebrates. Not only are they habitats of high biodiversity, they are also vital for the reproduction and recruitment of invertebrates, and are likely to be important refugia for invertebrates during spates and from fish.

There appeared to be little functional difference for invertebrates between different types of vegetated margin, although, as described previously, some snails, bugs and small fish favoured the margins of grazed stretches. Other taxa, however, favoured the more diverse margins found in ungrazed stretches, where few differences in invertebrate communities were found, despite apparently marked differences in physical nature of marginal plants, *viz.*, reeds and *Apium*. One important finding is that margins consisting of the trailing stems and leaves of terrestrial vegetation can be as valuable a habitat for most invertebrates as semi-emergent aquatic vegetation. They may function as a direct pathway from the water to the land and vice versa, and thus be a particularly valuable habitat for those species that travel between the two 'biotopes' at some point of their lives. The benefit of leaving such vegetation has important resource-saving implications for bankside managers, particularly on streams where margins are managed needlessly via routine mowing, annual clearance programs and weed control.

Marginal vegetation was also shown to have another important role - that of an invertebrate refuge from fish predation and high flows. The first years' survey showed that, in this respect, all marginal vegetation plays a vital part. Wright (1993) speculates that tall emergent perennial macrophytes may offer critical refugia during severe physical conditions. This Bankside project has also shown that dead bankside vegetation, left trailing in the water from the previous year, can support diverse and abundant invertebrate assemblages. It is also persistent - those habitats sampled in May consisted of dead over-wintered vegetation. This overhanging vegetation is particularly important in reaches where it is dominant due to the rarity of macrophytes, such as in woodlands. In streams with few marginal macrophytes, perhaps due to the nature of the bank, the hydraulic regime, channel management or shade from overhanging trees, the overhanging stems and leaves of terrestrial bankside vegetation can provide an important substitute. Such vegetation is able to ameliorate the effects of high winter flow conditions for invertebrates by providing areas of structural stability and reduced water velocities. Borchardt (1993) states that restoration projects should consider hydraulic disturbances at high flow to be of significance for benthic invertebrates, and adds that every increase in refugial space appears to mitigate the impact of critical hydraulic stress. Additionally, this vegetation may well confer substantial protection from scour erosion upon the bank itself, especially where woody stems are involved (Morgan *et al.*, 1999). Its clearance may thus be potentially damaging to bank structure, as well as invertebrate biodiversity.

Marginal habitat would therefore appear to function as well with dead vegetation as with live, as the abundance of invertebrates in winter did not show a great decline. It is thus likely that the presence/absence of marginal vegetation may be more important than its extent, particularly for those species only briefly associated with margins, perhaps for emergence, or following oviposition by adults. The caddis and beetles, in particular, were as abundant in the sparse woodland margins as they were in the wider grazed and ungrazed margins. This may be due to the fact that the margins 'function' is provided by only a small quantity of that habitat, for example that needed for oviposition or refuge from flow or fish. Small limnephilid caddis were especially abundant in all margins in January, following oviposition by adults, despite differences in the extent of vegetation. Presumably the simple presence of emergent vegetation or overhanging stems and leaves is sufficient to enable caddis adults to oviposit along the margins. These margins are also an essentially temporary habitat for the larvae of caddis species like *Potamophylax* and *Halesus* spp. which subsequently move out to other habitats in the middle of streams.

In addition, marginal areas are likely to provide a generally discrete area for predation avoidance. Work with *Gammarus* and Bullhead demonstrated the value of *Apium* as an invertebrate refuge, a feature which is highly likely to stabilise population fluctuations for both sets of animals by reducing the invertebrate vulnerability. Therefore, wetted marginal vegetation should be seen as an essential component of all watercourses, in the form of fresh emergent macrophytes such as *Apium* and/or 'fallen-in' riparian plants like dead reeds and *Oenanthe*. It must be made clear that the extent of this vegetation need not reach such levels where flood defence measures are jeopardised, but neither should these latter considerations be allowed to prescribe complete removal of marginal vegetation, especially at vulnerable times of year like winter.

Botanical diversity of margins may not therefore be as important as diversity of terrestrial plant structure along the banks. The terrestrial nature of the margins should also be considered in comparisons of different types of marginal vegetation. Although reeds may not have as great an invertebrate abundance or diversity as, say, *Apium* in ungrazed reaches, the aerial part of reeds may be of great use to species with winged adults. These latter may use banks of reeds as swarming sites, emergence sites, resting places and oviposition sites (pers. obs. Brachycentridae caddis on reeds beside the R. Frome). The wide, flat surfaces of reeds were often found to have large numbers of eggs on them, including clusters of beetle and dipteran eggs (although no analysis of distribution between different margins was undertaken). Thus, different margins may have different functional roles. More research is required to elucidate these fine-scale differences, should they exist.

This study, and others (Armitage & Cannan, 1998), has demonstrated the high importance of stream margins relative to the mid-channel habitats of coarse gravel and *Ranunculus* beds. Although all habitats are physically and biologically inter-linked and cannot be considered independently of the others, chalk-stream conservation management should perhaps focus on marginal areas as centres of biodiversity, rarity and reproduction. Projects that aim to improve mid-channel substrate at the expense of well-developed marginal vegetation may reduce, rather than improve, the conservation value of the stretch. Re-creating conditions under which marginal vegetation can flourish should thus assume significant importance in stream restoration projects. Encouraging the rapid return of natural marginal vegetation in sections of stream that have been re-sectioned or have been re-dug into a more natural, meandering course (Biggs *et al.*, 1998) is likely to allow quicker recovery of diverse and abundant macroinvertebrate communities.

9.6 Vertebrate wildlife

Included within the project's original proposal was the discretionary examination of the effect that various bankside management regimes have upon mammals, bird-life, and fish. The main body of work was however concentrated on aquatic invertebrates. The distribution of small river fish such as minnows and sticklebacks was considered where they were caught incidental to invertebrate sampling, or where informal observation offered an insight into their behaviour. Larger river fish, riverine mammals and associated birds were not studied, there is however a wealth of information on these subjects (e.g. RSPB, NRA & RSNC, 1994).

Features required for successful river management are generally accepted, although the specifications may vary depending on the organism (or group of organisms) being accommodated. Mammals are generally sensitive in their requirements, not only in terms of suitable habitat but also with regard to disturbance and pollution. In addition, the large areas of 'quality' riverbank required to attract animals such as otters means management must often be species-specific. However, a common requirement in mammal habitat management is the necessity of bankside vegetation. Although water shrews and voles prefer certain bank profiles and flow regimes, the presence of tall herbs, thickets and scrub etc. is essential to provide cover, and thus protection from predation. Marginal trees also appear highly important, as demonstrated by an otter survey on the River Tiefi, which revealed that 82% of 33 known holts were in the roots of marginal trees (G. Liles, pers. comm., in Mason *et al.* 1984). In addition, some trees appear more suitable than others – the root systems of oak, ash and sycamore spread horizontally, rather than downwards in a mesh as with alder and some willows.

For many of the birds that use rivers as breeding and feeding grounds, marginal vegetation in the form of aquatic macrophytes, terrestrial herbs, scrub and trees is a fundamental component – providing cover, food (insects and seeds etc.) and nesting sites. Although limited livestock access along certain reaches can produce muddy margins beneficial for wading birds, removal of woodland, bankside scrub and overwintered vegetation through grazing or agricultural cultivation will dramatically reduce the suitability of a river stretch for many bird species.

Fish requirements are often summarised in terms of water quality, hydraulics and substrate for spawning. From personal observation and recent research by the Game Conservancy Trust, however, it is clear that trout and salmon are considerably more abundant in ungrazed (fenced) sections of stream than in adjacent grazed areas. Pinder (1997) states that cutting of marginal macrophytes should be avoided to provide shelter [for fish] from high current velocities, spawning habitat and enhanced feeding conditions for young fish generally. He suggests that where this is not possible for reasons of flood defence, opposite banks should be cut in alternate years. Trees are also important bankside features for fish, providing shade, flow diversity where branches or trees fall in, and invertebrate input. Terrestrial input of invertebrates from trees alone has been estimated to possibly exceed within-stream production of benthic invertebrates at certain times of year (Mason & Macdonald, 1982) making these areas significant providers of food items for fish. However, personal observation of the shallow, warm and silty margins of grazed fields showed these too to be important areas for young minnow fry and sticklebacks.

Bats have also received attention from river managers. Requirements for Daubenton's Bat have been described in detail with respect to riparian vegetation: 'Stretches of a river containing pools with a smooth flowing surface should be maintained or created particularly where trees are present on both sides. Riverside woodland corridors and woodland areas close to rivers should be maintained or created to encourage a diversity of insect species' (British Wildlife, Vol.10, No.1). The necessity for long stretches of bankside vegetation appears common for the species associated with watercourses (Daubenton's, Natterer's, whiskered, noctule and pipistrelle bats) (RSPB, NRA & RSNC, 1994) – mainly because vegetation of this nature yields an abundance of diverse insect prey.

9.7 Links with River Habitat Survey (RHS)

The RHS is able to provide baseline data on the current state of over 5,600 river and stream sites across the UK. Besides reporting specific statistics on riverine features it is capable of identifying areas (e.g. individual sites, catchments and regions) of particular habitat value for wildlife. Rare features within a region, or rare combinations of features for a particular river type can be identified.

In this respect RHS is able to highlight and monitor areas requiring conservation management, by providing a huge range of detail on the physical aspects of river corridors, including riparian (bankside) land-use. For instance, data produced by the Survey shows that 26.5% of semi-natural chalk river sites had a significant amount of ploughed agricultural land adjacent to the watercourse. 65% of chalk rivers had tall herbs present at some point along their banks whereas this type of vegetation was only present on 34.5% of small, lowland riffle-dominated rivers. Continuous trees on either bank were only present at <15% of chalk river sites (Data from Raven *et al.*, 'River Habitat Quality', 1998). When information like this can be linked to the findings of specific projects (e.g. the importance of the 'bankside' for invertebrates) it becomes an important management tool. RHS information can thus be used as a benchmark for management policy, perhaps indicating areas where rehabilitation would, or would not, enhance an existing combination of characteristics and allow the potential introduction of absent species. Detailed ecological information on marginal biota that identifies quantitative relationships between 'animal and habitat' would thus provide the necessary link between RHS and instream surveys.

In addition, RHS would doubtless prove to be a powerful tool in locating regions of the country where further assessment of the importance of bankside and marginal vegetation should be carried out – for example, locations with many impacted watercourses such as East Anglia.

9.8 Non chalk-stream systems

All of the work in this project has focused on chalk streams and rivers in Dorset. These streams support exceedingly rich and diverse communities of plants and animals (Mainstone *et al.*, 1998). This is a product of a specific geology resulting in clean and stable flow regimes, a predominant lack of urbanisation and harmful channel modification, and diverse 'semi-natural' riparian management. How the findings described in this report may relate to rivers in other parts of the country requires consideration. In general terms, the conclusions relating to the value of certain margins and bankside management regimes are relevant to all watercourses, however further information is needed before these can be applied to non chalk stream systems. Greater national coverage and assessment of the value of riparian and marginal vegetation would be a logical and practical step forward - clay catchments, upland areas, plus sites which have been heavily impacted and/or degraded are examples of systems which might be considered.

It is also apparent that much of the work in this project was concentrated on small to medium sized channels, where the role of marginal aquatic- and bankside-vegetation has been shown to be highly important. There is a need to extend this work to larger watercourses (width >10m) where the effect of riparian changes, and the amount of marginal vegetation, may have different influences on the aquatic invertebrate fauna. In larger rivers, compared to small streams, areas of marginal vegetation may be more important for invertebrates relative to benthic habitats. Deep rivers can prevent sufficient sunlight penetrating to the mid-channel substrata, and they therefore often lack aquatic macrophytes (plus the cover and periphytic algae that these provide) except at the margins. Recent work on the River Great Ouse (a highly eutrophic, regulated, slow-flowing lowland river) has shown that side channels support a much more diverse and abundant biota than the main river, mainly as a result of increased habitat diversity (Pinder *et al.*, 1997). The specific role that marginal areas and side channels play in these cases requires closer investigation.

Permeable geology and aquifer-fed water supplies tend to ensure that catastrophic (*sensu* Borchardt, 1993) spates do not occur in chalk-streams. However, many small streams running over largely impermeable geology record spate-flows in synchrony with rainfalls. This can hinder or prevent marginal vegetation and invertebrate communities establishing themselves to any great extent, and sweep out emergent vegetation that has grown. This can lead to a situation where small channels act primarily as water-conduits rather than wildlife corridors. The value of potentially suitable 'dry' riparian vegetation thus becomes subordinate to the flow characteristics, which are dictated by the underlying catchment geology. In these cases however, marginal vegetation left trailing in the water from banksides may assume vital relative-importance for invertebrate communities, due to the lack of other refugia. The feasibility of directed bankside management on such streams again requires assessment.

9.9 Conclusions and Recommendations

It is clear that good management of stream and river banksides is a major contributing factor in the achievement of a diverse and abundant aquatic invertebrate community. This work on chalk-streams has highlighted the fundamental nature of aquatic marginal vegetation, and described the importance of different bankside environments. Further recognition of the importance of these areas would aid considerably in meeting specific Environment Agency (EA) goals related to rivers, such as those laid out in EA Functional Action Plans and the UK Biodiversity Action Plan, for example:

- Conservation and enhancement of biodiversity
- Improvement of river landscapes
- Promotion of wildlife habitats
- Provision of conservation benefits through natural processes

On smaller rivers and streams in particular where severe flooding is rare (and where past practices to alleviate flood risk have led to degraded bankside habitat and vegetation structure) encouraging botanical communities to re-establish would enable the statutory obligations listed above to be met whilst maintaining awareness of potentially conflicting interests. The monitoring of invertebrate community changes in response to a realistic bankside management program that satisfies both Conservation and Flood Defence interests and Action Plan aims would seem an obvious future study.

In degraded river systems, bankside vegetation (both aquatic and terrestrial) is likely to be of even greater importance. Chalk streams support exceedingly rich and diverse communities of plants and animals (Mainstone *et al.*, 1998), unique recognition of which, in terms of rivers, has been denoted by preparation of Biodiversity (Habitat) Action Plans. Yet even so, habitats can be prioritised, and the presence of a natural riparian and marginal environment has emerged as paramount. In less productive watercourses, and those that have been insensitively managed in the past, such physical habitat is often largely absent. This is likely to render any remaining areas of bankside/marginal vegetation of vital significance. In order that objectives concerning the conservation of natural resources, animals and plants etc. can be met, this work would urge that such areas are -

- Monitored, to assess their importance with regard to associated invertebrate communities
- Protected from detrimental practices or events
- Encouraged, by sympathetic management

The project findings relate to the streams and rivers on which the work was carried out, and practical assessment of their applicability, at this stage, to other types of watercourse is required. Ecologically damaging practices such as bank-toe mowing, severe grazing and annual macrophyte clearance have been similarly recognised by wider studies (Ward *et al.*, 1998) as detrimental. It is therefore expected that best environmental practice for river habitat protection and restoration, as revealed by this study, would be similar nation-wide. Accordingly, it is suggested that attention be focused on the following Best Practice Guidelines:

- **Reduction of severe bankside damage by cattle, thereby**
  - improving bank integrity, with morphological and ecological implications
  - producing intermittent reaches where light-grazing leads to characteristic poached margins, which are beneficial to snails, bugs and fly-larvae

- **Enhancement of the instream marginal environment**
  - by encouraging a heterogeneous aquatic macrophyte community
  - by allowing dead or senescent trailing ('fallen-in') terrestrial vegetation to overwinter, particularly where other refugia cover is absent

- **Encouraging the return of marginal vegetation where it is absent**
  - by reducing cattle access, by restructuring steep banks to a more favourable profile and/or by minimising unnecessary human disturbance e.g. frequent mowing, thereby creating structural diversity of water-edge habitat of benefit to fish and invertebrates.

- **The promotion of 'complex' riparian habitat**
  - creating floristically diverse areas of mixed structure and height etc. advantageous to adult invertebrates, birds and riverine animals such as voles
  - allowing patches of scrub and woodland to develop for similar faunal benefit

This project has determined recommendations for bankside management (for invertebrates) based on sound scientific investigation. It has also revealed the amount of research still required, at the specific level of topics such as the location of beetle pupation sites, to assessment of the 'critical amount' of particular vegetation types that are required to sustain an ecologically dynamic riparian system. In addition, further work in alternative catchment areas is essential to determine, for example, whether in-situ management practices for plants, birds and fish etc. concur with invertebrate requirements, and to assess the importance of 'habitat-islands' in watercourses with impoverished bankside vegetation. An understanding of the functional ecology of riparian margins would seem to be an essential ingredient in the link between invertebrate and bankside management. It is hoped that the main findings, summarised below, will contribute to decision-making processes and stimulate further investigation and research.

- *Areas of wetted marginal vegetation are extremely important components of the riverine environment in all chalk-stream riparian management regimes in terms of aquatic invertebrate biodiversity, abundance, rare species and reproduction.*

- *The emergent adult life-stage of many aquatic invertebrates may require as much attention as the larval stage. Best management should aim at maximising the variety of bankside vegetation structure, and recognise the significance of ungrazed sections and woodland.*

10. REFERENCES

Andersen, T. H., Hansen, H. O., Iversen, T. M., Jacobsen, D., Krojgaard, L. & Poulsen, N. (1992). Growth and feeding of 0+ brown trout (*Salmo trutta* L.) introduced to two small Danish streams. *Archiv für Hydrobiologie*, **125**, 339-346.

Anderson, N. H., 1974: The eggs and oviposition behaviour of *Agapetus fuscipes* Curtis (Trich. Glossosomatidae). - *Entomologist's Monthly Magazine* 109: 129-131.

Anderson, R. V. & Day, D. M. (1986). Predictive quality of macroinvertebrate – habitat associations in lower navigation pools of the Mississippi River. *Hydrobiologia*, **136**, 101-112.

Armitage P. D. & Cannan C. E. (1998) Nested multi-scale surveys in lotic systems - tools for management. In: Bretschko, G. & Helesic, J. (Eds.) Advances In River Bottom Ecology. Backhuys Publishers, Leiden, 293-314.

Armitage, P. D., Pardo, I. & Brown, A. (1995). Temporal constancy of faunal assemblages in 'mesohabitats'. Applications to management? *Archiv für Hydrobiologie*, **133**, 367-387.

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

Bass, J. (1998). Last-instar larvae and pupae of the *Simuliidae* of Britain and Ireland: A key with brief ecological notes. FBA Scientific Publication No. 55.

Bechara, J. A., Moreau, G. & Planas, D. (1992). Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2093-2103.

Bechara, J. A., Moreau, G. & Planas, D. (1993). The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community, the role of spatial and size refugia. *Journal of Animal Ecology*, **62**, 451-464.

Behmer, D. J. & Hawkins, C. P. (1986). Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwater Biology*, **16**, 287-300.

Berrie, A. D. (1992). The chalk-stream environment. *Hydrobiologia*, **248**, 3-9.

Biggs, J., Corfield, A., Gron, P., Hansen, H. O., Walker, D., Whitfield, M. & Williams, P. (1998). Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, V – Short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 241-255.

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

Bronmark, C. (1988). Effects of vertebrate predation on freshwater gastropods: an exclosure experiment. *Hydrobiologia*, **169**, 363-370.

Brookes, A. & Shields, F. D. Jr. (Eds., 1996). River channel restoration: guiding principles for sustainable projects. Wiley.

Brown, C. L., Poe, T. P., French, J. R. P. III, Scloesser, D. W. (1988). Relationships of phytomacrofauna to surface area in naturally occurring macrophyte stands. *Journal of the North American Benthological Society*, 7, 129-139.

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

Bunn, S. E. & Hughes, J. M. (1997). Dispersal and recruitment in streams: evidence from genetic studies. *Journal of the North American Benthological Society*, **16**, 338-346.

Castro, L. B. (1975). Okologie und productionsbiologie von *Agapetus fuscipes* Curt. im Breitenbach 1971-1972. *Archiv für Hydrobiologie Supplementband*, **45**, 305-375.

Chilton, E. W. II (1990). Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria americana*) in Lake Onalaska, Wisconsin. *Journal of Freshwater Ecology*, **5**, 455-466.

Cogerino, L. Cellot, B. & Bournaud, M. (1995). Microhabitat diversity and associated macroinvertebrates in aquatic banks of a large European river. *Hydrobiologia*, **304**, 103-115.

Collier, K. J., Smith, B. J. and Baillie, B. R. (1997). Summer light-trap catches of adult Trichoptera in hill-country catchments of contrasting land use, Waikato, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **31**, 623-634.

Collier, K. J., Smith, B. J. (1998). Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, **361**, 53-65.

Cooper, S. D. (1988). The responses of aquatic insects and tadpoles to trout. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 1698-1703.

Cranston, P. S., Ramsdale, C. D., Snow, K. R. & White, G. B. (1987). Keys to the adults, male hypopygia, fourth-instar larvae and pupae of the British mosquitoes (*Culicidae*) with notes on their ecology and medical importance. FBA Scientific Publication, No. 48.

Crowder, L. B. & Cooper, W. E. (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, **63**, 1802-1813.

Cummins, K. W., Wilzbach, M. A., Gates, D. M., Perry, J. B. & Taliaferro, W. B. (1989). Shredders and riparian vegetation. *Bioscience*, **39**, 24-30.

Cyr, H. & Downing, J. A. (1988). The abundance of phytophilous invertebrates on different species of submerged macrophytes. *Freshwater Biology*, **20**, 365-374.

Dawson, F. H. (1976). Organic contribution of stream edge forest litter fall to the chalk stream ecosystem. *Oikos*, **27**, 13-18.

Diehl, S. (1992). Fish predation and benthic community structure: The role of omnivory and habitat complexity. *Ecology*, **73** (5), 1646-1661.

Downes, J. A. (1969). The swarming and mating flight of Diptera. *Annual Review of Entomology*, **14**, 271-298.

Drake, C. M. (1995). The effects of cattle poaching on insects living at the margin of the River Itchen, Hampshire. *British Journal of Entomology & Natural History*, **8**, 165-169.

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

Dudley, T. (1988). The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 1153-1158.

Dvorak J. & Best, E. P. H. (1982). Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. *Hydrobiologia*, **95**, 115-126.

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

Eklov, P. (1997). Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1520-1531.

Elliott, J. M. (1977). A key to the larvae and adults of British freshwater Megaloptera and Neuroptera. Freshwater Biological Association Scientific Publication No. 35.

Enders, G. & Wagner, R. (1996). Mortality of *Apatania fimbriata* (Insecta, Trichoptera) during embryonic, larval and adult life stages. *Freshwater Biology*, **36**, 93-104.

Fitter, R. & Manuel, R. (1986). *A Field Guide to Freshwater Life of Britain and North-West Europe*. Collins, London.

Friberg, N., Kronvang, B., Hansen, H. O., & Svendsen, L. M. (1998). Long-term, habitat-specific response of a macroinverbrate community to river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 87-101.

Friberg, N., Kronvang, B., Svendsen, L. M., Hansen, H. O., Nielsen, M. B. (1994). Restoration of a channelized reach of the river Gelsa, Denmark: effects on the macroinvertebrate community. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **4**, 289-296.

Game Conservancy Trust leaflet: Restoring the River Piddle – results of research by the Game Conservancy Trust and Dr. Nick Giles & Associates.

Garner, P., Clough, S., Griffiths, S. W., Deans, D., Ibbotson, A. (1998). Use of shallow marginal habitat by *Phoxinus phoxinus*: a trade-off between temperature and food? *Journal of Fish Biology*, **52**, 600-609.

Gibbons, D. W. & Pain, D. (1992). The influence of river flow rate on the breeding behaviour of Calopteryx damselflies. *Journal of Animal Ecology*, **61**, 283-289.

Giles, N. & Summers, D. W. (1996). *Helping fish in lowland streams.* Game Conservancy Ltd. Fordingbridge.

Gilinsky, E. (1984). The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology*, **65**, 455-468.

Glime, J. M. & Clemmons, R. M. (1972). Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. *Ecology*, **53**, 458-464.

Gore, J. A. (Ed) (1985). The restoration of rivers and streams: theories and experience. Butterworth.

Gortz, P. (1998). Effects of stream restoration on the macroinvertebrate community in the river Esrom, Denmark. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 115-131.

Gregg, W. W. & Rose, F. L. (1985). Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia*, **128**, 45-56.

Gunn, R. J. M. (1985). The biology of *Brachycentrus subnubilus* Curtis (Trichoptera) in the River Frome, Dorset. *Hydrobiologia*, **120**, 133-140.

Hansen, H. O. & Madsen, B. L. (Eds., 1997). River restoration '96 – Plenary lectures. International Conference arranged by the European Centre for River Restoration. National Environmental Research Institute, Denmark.

Harper, D. & Everard, M. (1998). Why would the habitat-level approach underpin holistic river survey and management? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 395-413.

Harper, D., Ebrahimnezhad, M., Climente I. & Cot, F. (1998). Artificial riffles in river rehabilitation: setting the goals and measuring the successes. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **8**, 5-17.

Harper, D., Smith, C., Barham, P. & Howell, R. (1995). The ecological basis for the management of the natural river environment. *In*: Harper, D. & Ferguson, A.J.D. (*Eds.) The ecological basis for river management.* pp. 219-238. Wiley & Sons, Chichester, UK.

Harper, D., Smith, C., Barham, P. (1992). Habitats as the building blocks for river conservation assessment. *In*: Boon, P.J., Calow, P. & Petts, G.E. (*Eds.) River conservation and management.* pp. 311-319. Wiley & Sons, Chichester, UK.

Harrison, S. S. C. & Hildrew, A. G. (1998). Distribution dynamics of epilithic insects in a lake littoral. *Archiv für Hydrobiologie,* In Press.

Harrod, J. J. (1964). The distribution of invertebrates on submerged aquatic plants in a chalk stream. *Journal of Animal Ecology,* **33**, 335-348.

Hawkins, C. P., Murphy, M. L., Anderson, N. H. (1982). Effects of canopy structure, substrate composition and gradient on the structure of macroinvertebrate communities in cascade range streams of Oregon. *Ecology,* **63**, 1840-1856.

Hildrew, A. G. & Townsend, C., 1987: Organization in freshwater benthic communities. – In: Gee, J. & Giller, G. (Eds.) *Organization of Communities: Past and Present*: 347-371. - Blackwell Scientific publications, Oxford.

Hill, M. O. (1979). TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics.* Cornell University, Ithaca, New York.

Jackson, J. K. & Resh, V. H. (1989). Distribution and abundance of adult aquatic insects in the forest adjacent to a northern Californian stream. *Environmental Ecology,* **18**, 278-283.

Jacobsen, D. & Sand-Jensen, K. (1992). Herbivory of invertebrates on submerged macrophytes from Danish freshwaters. *Freshwater Biology,* **28**, 301-308.

Jenkins, R. A., Wade, K. R. & Ough, E. (1984). Macroinvertebrate-habitat relationships in the River Teifi catchment and the significance to conservation. *Freshwater Biology,* **14**, 23-42.

Jones, N. V. (1974). The Trichoptera of a stony shore of a lake with particular reference to *Tinodes waeneri* (L.) (Psychomyiidae) –*In*, Malicky, H. (*Ed.*) *Proceedings of the First International Symposium on Trichoptera* pp. 117-131. Dr. W. Junk. The Hague.

Kornijow, R., Gulati, R. D., Ozimek, T. (1995) Food preference of freshwater invertebrates: comparing fresh and decomposed angiosperm and a filamentous alga. *Freshwater Biology*, **33**, 205-212.

Ladle, M. & Westlake, D. F. (1995). River and Stream Ecosystems of Great Britain. – *In*: Cushing, C. E., Cummins, K.W. & Minshall, G.W. (*Eds*.). *River and stream ecosystems.* Elsevier, New York.

Lauridsen, T. L. & Lodge, D. M. (1996). Avoidance by *Daphnia magna* of fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. *Limnology and Oceanography,* **41**, 794-798.

Macan, T. T. & Worthington, E. B. (1968). *Life in Lakes and Rivers.* Collins, London.

Macan, T. T. (1961). Factors that limit the range of freshwater animals. *Biological Reviews,* **36**, 151-198.

Macan, T. T. (1962). Ecology of aquatic insects. *Annual Review of Entomology*, **7**, 261-286.

Macan, T. T. (1977). A twenty-year study of the fauna in the vegetation of a moorland fishpond. *Archiv für Hydrobiologie,* **81**, 1-24.

Mackey, A. P. & Berrie, A. D. (1991). The prediction of water temperatures in chalk streams from air temperatures. *Hydrobiologia,* **210**, 183-189.

Mainstone, C. P., Holmes, N .T., Armitage, P. D., Wilson, A. M., Marchant, J. H., Evans, K. & Solomon, D. (1998) Chalk Rivers - Nature Conservation and Management. Consultation Draft Report to English Nature and the Environment Agency.

Mann, R. H. K., Blackburn, J. H. & Beaumont, W. R. C. (1989). The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology*, **21**, 57-70.

Mason, C. F. & Macdonald, S. M. (1982). The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology*, **12**, 305-311.

Mason, C. F., Macdonald, S. M. & Hussey, A. (1984). Structure, management and conservation value of the riparian woody plant community. *Biological Conservation*, **29**, 201-216.

Maurer, M. A. & Brusven, M. A. (1983). Invertebrate abundance and colonization rate in *Fontinalis neo-mexicana* (Bryophyta) in an Idaho Batholith stream, U.S.A. *Hydrobiologia*, **98**, 9-15.

Minshall, G. W. (1989). Aquatic insect-substratum relationships. *In*: Resh, V.H. & Rosenburg, D.M. (*Eds*.) *The ecology of aquatic insects*. pp. 358-400. Praeger Press, New York.

Morgan, R. P. C., Collins, A. C., Hann, M. J., Dunderdale, J. A. L. & Gowing, D. J. G. (1999). Waterway bank protection: a guide to erosion assessment and management. Environment Agency Publication 11, The Stationery Office.

Newman, R. M. (1991). Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society*, **10**, 89-114.

Newman, R. M., Kerfoot, W. C. & Hanscom, Z. (1996). Watercress allelochemical defends high-nitrogen foliage against consumption: effects on freshwater invertebrate herbivores. *Ecology*, 77, 2312-2323.

Newson, M. D., Harper, D. M., Padmore, C. L., Kemp, J. L. & Vogel, B. (1998). A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 431-446.

Olson, E. J., Engstrom, E. S., Doeringsfeld, M. R. & Bellig, R. (1995). Abundance and distribution of macroinvertebrates in relation to macrophyte communities in a prairie marsh, Swan Lake, Minnesota. *Journal of Freshwater Ecology*, **10**, 325-335.

Ormerod, S. J. Wade, K. R. & Gee, A. S. (1987). Macro-floral assemblages in upland Welsh streams in relation to acidity and their importance to invertebrates. *Freshwater Biology*, **18**, 545-557.

Ormerod, S. J., Rundle, S. D., Lloyd, E. C. & Douglas, A. A. (1993). The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. *Journal of Applied Ecol.*, **30**, 13-24.

Ormerod, S. J., Weatherley, N. S. & Merrett, W. J. (1990). The influence of conifer plantations on the distribution of the golden ringed dragonfly *Cordulegaster boltoni* (Odonata) in upland Wales. *Biological Conservation*, **53**, 241-251.

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

Osbourne, L. L. & Kovacic, D. A. (1993). Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, **29**, 243-258.

Palmer, C. G., O'Keefe, J. H. & Palmer, A. R. (1991). Are macroinvertebrate assemblages in the Buffalo River, southern Africa, associated with particular biotopes? *Journal of the North American Benthological Society*, **10**, 349-357.

Pardo, I. & Armitage, P. D. (1997). Species assemblages as descriptors of mesohabitats. *Hydrobiologia*, **34**, 11-128.

Penczak, T. (1995). Effects of removal and regeneration of bankside vegetation on fish population dynamics in the Warta River, Poland. *Hydrobiologia*, **303**, 207-210.

Appendix 2

In the following Appendix of Raw Data (abundance & diversity) the pages are divided firstly by season (May, July, September & January) and secondly by management regime (grazed, ungrazed and woodland). Hence May/Grazed is followed by May/Ungrazed, May/Wood, then July/Grazed, July/Ungrazed and so on. Column headings provide this information by abbreviation, where:

Grazed	G
Ungrazed	U
Woodland	W

Main channel gravel	Gv
Ranunculus	Ra
Margin	M
Apium	A
Overhanging vegetation	OH
Reeds	Re
Grass	Gr
Grass + *Apium*	GA

Thus U/Gv represents main-channel gravel in an ungrazed reach. The column headings also show the name of the stream sampled.

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

Samways, M. J. & Steytler, N. S. (1996). Dragonfly (Odonata) distribution patterns in urban and forest landscapes and recommendations for riparian management. *Biological Conservation,* **78**, 279-288.

Sand-Jenssen, K. & Madsen, T. V. (1989). Invertebrates graze submerged rooted macrophytes in lowland streams. *Oikos,* **55**, 420-423.

Sand-Jenssen, K., Jeppersen, E., Nielsen, K., Van Der Bijl, L., Hjermind, L., Nielsen, L. W., Iversen, T. M. (1989). Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology,* **22**, 15-32.

Scheffer, M., Achterberg, A. A. & Beltman, B. (1984). The distribution of macro-invertebrates in a ditch in relation to the vegetation. *Freshwater Biology,* **14**, 367-370.

Schramm, H. L. & Jirka, K .J. (1989). Effects of aquatic macrophytes on benthic macroinvertebrates in two Florida lakes. *Journal of Freshwater Ecology,* **5**, 1-12.

Solem, J. O (1984). Adult behaviour of North American caddisflies. *In,* Morse, J. (*Ed.*) *Proceedings of the Fourth International Symposium on Trichoptera* pp. 375-382. Dr. W. Junk. The Hague.

Soska, G. J. (1975). Ecological relations between invertebrates and submerged macrophytes in the lake littoral. *Ekologia Polska,* **23**, 393-415.

Stanford, J. A., Ward, J. V., Liss, W. J., Frissell, C. A., Williams, R. N., Lichatowitch, J. A. & Coutant, C. C. (1996). A general protocol for restoration of regulated rivers. *Regulated Rivers Research and Management,* **12**, 391-413.

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

Statzner, B. (1977). The effects of flight behaviour on the larval abundance of Trichoptera in the Schierenseebrooks (North Germany). *In,* Crichton, M. (*Ed.*) *Proceedings of the Second International Symposium on Trichoptera* pp. 121-135. Dr. W. Junk. The Hague.

Suren, A. M. (1991). Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwater Biology,* **26**, 399-418.

Sweeney, B. W. (1993). Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. *Proceedings of The Academy of Natural Sciences of Philadelphia,* **144**, 291-340.

Ter Braak, C. J. F. (1987). CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondance analysis, principal components analysis and redundancy analysis. ITI-INO, Wageningen, The Netherlands.

Thienemann, A. (1950). Verbreitungsgeschichte der Sußwassertierwelt Europas. *Die Binnengwasser* Bd. 18, pp. 43-44. Stuttgart.

Townsend, C. R. (1996). Invasion ecology and ecological impacts of brown trout Salmo trutta in New Zealand. *Biological Conservation*, **78**, 13-22.

Tozer, W. E., Resh, V. H. & Solem, J. O. (1980). Bionomics and adult behaviour of a lentic caddisfly, *Nectopsyche albida* (Walker). *American Midland Naturalist*, **106**, 133-144.

Verdonschot, P. F. M. & Higler, L. W. G. (1989). Macroinvertebrates in Dutch ditches: a typological characterisation & the status of the Demmerik Ditches. *Hydrobiological Bulletin*, **23**, 135-142.

Vincent, B., Lafontaine, N. & Caron, P. (1982). Facteurs influencant la structure des groupements de macrinvertébrés benthiques et phytophiles dans la zone littorale du Saint-Laurent (Québec). *Hydrobiologia*, **97**, 63-73.

Vought, L. B-M., Kullberg, A. & Petersen, R. C. (1998). Effect of riparian structure and channel morphometry on detritus processing in channelized and natural woodland streams in southern Sweden. *Aquatic Conservation, Marine and Freshwater Ecosystems*, **8**, 273-285.

Wallace, I. D., 1991: A review of the Trichoptera of Great Britain. *Research and Survey in Nature Conservation*: No. 32. Nature Conservancy Council, Peterborough

Ward, D. E., Holmes, N. T. H., Andrews, J. H., Gowing, D. J. G. & Kirby, P. (1998). Environmental guidelines for vegetation maintenance in channel and on banks. Environment Agency R&D Technical Report W135.

Welton, J. S., Bass, J. A. B., Ladle, M. and Merrett, W. J. (1987). Distribution of oviposition sites and characteristics of egg development in the 'Blandford Fly' *Simulium posticatum* (Diptera, Simuliidae). *Journal of Applied Ecology*, **24**, 865-879.

Westlake, D. F., Casey, H., Dawson, H., Ladle, M., Mann, R. H. K., Marker, A. F. H. (1972). The chalk-stream ecosystem. *In*: Kajak, Z. & Hillbricht-Ilkowska (*Eds.*). *Productivity Problems of Freshwaters, Proceedings of the IBP-UNESCO Symposium on Productivity Problems of Freshwaters, Kazimierz Dolny, May 7-12, 1970*. PWN, Polish Scientific Publishers, Warsaw, pp. 615-635.

Whiles, M. R. & Wallace, J. B. (1997). Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. *Hydrobiologia*, **353**, 107-119.

Wiseman, S. W., Cooper, S. D. & Dudley, T. L. (1993). The effects of trout on epibenthic odonate naiads in stream pools. *Freshwater Biology*, **30**, 133-145.

Wohl, N. E. & Carline, R. F. (1996). Relations among riparian grazing, sediment loads, macroinvertebrates and fishes in three central Pennsylvania streams. *Canadian Journal of fisheries and Aquatic Sciences*, **53** (Supplement 1), 260-266.

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

Wright, J. F., Blackburn, J. H., Clarke, R. T. & Furse, M. T. (1994). Macroinvertebrate-habitat associations in lowland rivers and their relevance to conservation. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **25**, 1515-1518.

Wright, J. F., Blackburn, J. H., Westlake, D. F., Furse, M. T. & Armitage, P. D. (1992). Anticipating the consequences for river management for the conservation of macroinvertebrates. *In*: Boon, P.J., Calow, P. & Petts, G.E. (*Eds.) River conservation and management*. pp. 137-151. Wiley & Sons, Chichester, UK.

Wright, J. F., Cameron, A. C., Hiley, P. D. & Berrie, A. D. (1982). Seasonal changes in biomass of macrophytes on shaded and unshaded sections of the River Lambourn, England. *Freshwater Biology*, **12**, 271-283.

Wright, J. F., Clarke, R. T. & Blackburn J. H. (1993). Macroinvertebrates in lowland rivers in summer. A guide to macroinvertebrate-habitat associations. IFE unpublished report RL/T04053f5/4

Wright, J. F., Hiley, P. D. & Berrie, A. D. (1981). A 9-year study of the life cycle of *Ephemera danica* Mull. (Ephemeridae, Ephemeroptera) in the River Lambourn, England. *Ecological Entomology*, **6**, 321-331.

Wright, J. F., Hiley, P. D., Cameron, A. C., Wigham, M.E. & Berrie, A. D. (1983). A quantitative study of the macroinvertebrate fauna of five biotopes in the River Lambourn, Berkshire, England. *Archiv für Hydrobiologie*, **96**, 271-292.

11. APPENDICES

	Year 1	Year 2			Year 3	
Stream/River Site	Lower Bere Lower Piddle Middle Piddle Tadnoll Cerne Lewell Hooke* Devil's Brook* Wynford Brook* Milbourne Stream* [*discarded subsequently]	Piddle @ Waterston Bere Stream Tadnoll Brook	Piddle @ Waterston Bere Stream	Piddle @ Waterston Bere Stream Tadnoll Brook	Bere Stream @ Roke Farm	River Frome d/s River Laboratory
Experiments/ Aspects covered	Extensive invertebrate surveys, encompassing both the instream and bankside environments	Effect of woodland (using *Agapetus*)	Value of margins as refugia (6 exps.) (*Gammarus* / Bullhead / Depth)	Adult distribution (Malaise traps)	Factors affecting adult and larval distribution	Seasonal dynamics of the bankside habitat
Management regimes	Woodland Ungrazed, occasional trees Ungrazed, no trees Grazed	Woodland 'Near' trees 'Far' from trees	N/A	Woodland 'Near' trees 'Far' from trees	Woodland Open (ungrazed) (Open field – grazed)	Areas incorporating trees, open/ungrazed and grazed field
'Habitats' sampled	Main-channel gravel Main channel *Ranunculus* Overhanging marginal vegetation Wetted grass / *Apium* Reeds (instream & aerial parts) Bankside veg. (trees, herbs, grass)	Main-channel gravel		Bankside. Within woodland, ± 50m downstream, ± 200-250m downstream of woodland, at each site	Main-channel gravel Bankside vegetation Water column (drift)	Specific bankside sites
Replication	'Habitat' x 3 (where found) for each management type, per site	Spatially, x3 per area sampled, Temporally as below		Temporally, x 10	Varied between experiments. Temporally during the summer	23 sites, each sampled every 3 weeks
Sampling Technique	Kick Samples Terrestrial sweep-net	Surber sampling	Surber sampling	Malaise traps Sticky (fly-paper) traps	Sticky-traps, drift-traps, Sweep net, Surber samples	Aquatic kick/sweep samples
Sampling period	May / June (1996) July (1996) September (1996) January (1997)	May (1997) July (1997) September (1997) January (1998)	June – September (1997)	May – September (1997)	May/June – October (1998)	January 1998 – February 1999
Taxonomic level	Species (aquatic) Family (terrestrial)	Species	Species	Species (caddis), Family (others, incl. may- & stoneflies)	Family	Species

Appendix 2

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Reeds	Re
Grass	Gr
Grass + *Apium*	GA

Thus U/Gv represents main-channel gravel in an ungrazed reach. The column headings also show the name of the stream sampled.

MAY

ABUNDANCE	G/Gv Bere	G/Gv Cerne	G/Gv Lewell	G/Gv Lo Piddle	G/Ra Bere	G/Ra Cerne	G/Ra Lewell	G/Ra Lo Piddle	G/A Bere	G/A Lo Piddle	G/Gr Cerne	G/Gr Lewell	G/Gr Lo Piddle	G/GA Bere	G/GA Cerne	G/GA Lewell	G/GA Lo Piddle
COLEOPTERA	37.50	41.17	27.00	40.00	0.00	2.17	5.00	2.17	2.17	10.00	10.33	18.67	6.00	2.17	10.33	18.67	8.00
HEMIPTERA	0.00	0.00	0.00	0.00	0.00	0.00	4.33	0.33	13.67	25.17	20.17	13.83	60.83	13.67	20.17	13.83	43.00
TRICHOPTERA	8.17	20.00	21.00	56.17	7.17	13.00	64.83	43.67	33.67	101.50	24.83	36.00	88.00	33.67	24.83	36.00	94.75
CRUSTACEA	9.67	449.50	83.00	108.67	0.00	75.83	9.00	4.67	18.00	97.50	682.50	114.83	34.67	18.00	682.50	114.83	66.08
DIPTERA	88.00	24.33	162.50	64.17	1928.33	910.00	60.67	689.00	19.00	152.00	30.33	192.83	137.50	19.00	30.33	192.83	144.75
FISH	0.00	0.00	0.00	0.00	0.33	0.00	2.17	0.00	2.83	2.83	1.00	2.50	1.00	2.83	1.00	2.50	1.92
HIRUDINEA	12.67	8.17	6.50	2.50	2.17	0.00	0.00	0.00	8.17	0.00	2.50	1.00	0.00	8.17	2.50	1.00	0.00
EPHEMEROPTERA	605.17	279.67	31.67	102.83	775.67	1557.83	297.17	297.17	273.33	611.67	427.17	110.50	186.67	273.33	427.17	110.50	399.17
MOLLUSCA	10.83	22.33	28.83	9.00	2.17	8.67	22.67	2.50	6.00	55.50	112.17	60.67	10.17	6.00	112.17	60.67	32.83
ODONATA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
OTHER	24.17	49.83	110.50	21.67	2.17	10.83	299.00	30.33	13.33	13.00	299.33	56.33	17.67	13.33	299.33	56.33	15.33
PLECTOPTERA	0.00	0.00	0.00	16.50	0.00	0.00	0.00	0.00	2.17	2.50	0.00	0.00	0.00	2.17	0.00	0.00	1.25
TOTAL	796.17	895.00	471.00	421.50	2718.00	2578.33	764.83	1069.83	392.33	1072.67	1610.33	607.17	542.50	392.33	1610.33	607.17	807.58

NUMBER OF TAXA	G/Gv Bere	G/Gv Cerne	G/Gv Lewell	G/Gv Lo Piddle	G/Ra Bere	G/Ra Cerne	G/Ra Lewell	G/Ra Lo Piddle	G/A Bere	G/A Lo Piddle	G/Gr Cerne	G/Gr Lewell	G/Gr Lo Piddle	G/GA Bere	G/GA Cerne	G/GA Lewell	G/GA Lo Piddle
COLEOPTERA	4	4	2	2	0	1	2	1	1	4	6	5	4	1	6	5	4
CRUSTACEA	2	2	3	2	0	1	1	1	3	2	2	4	2	3	2	4	2
DIPTERA	7	4	5	5	2	2	2	3	6	4	5	7	6	6	5	7	5
EPHEMEROPTERA	6	4	4	4	3	2	3	4	3	4	2	2	3	3	2	2	4
FISH	0	0	0	0	0	0	1	0	2	2	1	2	1	2	1	2	2
HEMIPTERA	0	0	0	0	0	0	2	1	3	5	3	4	5	3	3	4	5
HIRUDINEA	3	3	2	1	1	0	0	0	3	0	2	1	0	3	2	1	0
MOLLUSCA	4	2	4	2	1	3	5	2	3	8	10	9	5	3	10	9	7
ODONATA	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
OTHER	2	3	2	3	1	1	2	1	1	1	3	3	2	1	3	3	2
PLECOPTERA	0	0	0	2	0	0	0	0	1	1	0	0	0	1	0	0	1
TRICHOPTERA	4	7	9	6	3	3	5	6	3	9	4	4	5	3	4	4	7
TOTAL	32	29	31	27	11	13	23	19	29	41	38	41	33	29	38	41	39

MAY

ABUNDANCE	U/Gv Bere	U/Gv Cerne	U/Gv Lewell	U/Gv Lo Piddle	U/Gv Mid Piddle	U/Gv Tadnoll	U/Ra Bere	U/Ra Cerne	U/Ra Lewell	U/Ra Lo Piddle	U/Ra Mid Piddle	U/Ra Tadnoll	U/Re Bere	U/Re Cerne	U/Re Lewell	U/Re Lo Piddle	U/Re Tadnoll
COLEOPTERA	40.75	114.50	43.67	74.33	34.67	49.67	4.83	18.58	8.67	14.58	18.00	9.33	3.17	5.58	19.83	14.67	2.50
HEMIPTERA	0.00	0.17	0.00	0.00	0.00	0.00	4.08	0.17	0.00	6.50	0.00	0.00	1.33	11.17	2.50	10.67	0.00
TRICHOPTERA	12.58	31.58	39.00	97.17	50.67	12.00	3.42	47.42	37.50	262.58	42.00	22.17	1.00	19.42	113.50	128.92	12.17
CRUSTACEA	32.83	98.75	186.33	175.83	156.00	34.67	2.50	137.58	186.33	20.17	37.17	9.67	17.50	80.67	69.33	37.42	23.83
DIPTERA	25.42	28.17	120.83	227.17	545.33	193.50	139.33	582.83	173.33	2208.92	2606.83	886.50	48.00	112.08	117.33	84.42	277.67
FISH	0.33	0.00	0.00	0.17	0.00	2.17	0.17	2.33	0.00	0.67	2.17	0.33	0.00	0.00	0.00	1.75	0.33
HIRUDINEA	9.83	3.67	3.17	0.50	2.17	0.00	0.00	0.00	2.17	0.83	0.00	0.00	0.00	1.08	2.17	3.17	0.00
EPHEMEROPTERA	638.00	462.42	46.17	234.08	1046.83	285.17	1922.00	1181.50	268.67	841.50	1235.67	598.67	158.83	274.75	212.33	137.67	156.00
MOLLUSCA	52.33	87.08	24.17	15.25	416.33	13.67	2.50	4.83	8.67	11.25	5.33	0.33	3.50	55.33	10.67	92.25	40.33
ODONATA	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.17	1.00	18.17	0.00
OTHER	8.08	31.00	528.67	93.50	169.67	190.50	13.00	125.67	149.50	50.92	71.50	292.50	8.67	52.67	86.67	17.33	1165.67
PLECTOPTERA	2.17	0.33	0.00	13.00	0.33	17.67	0.00	0.00	0.00	1.08	0.00	0.00	0.00	0.00	0.00	0.17	0.00
TOTAL	822.33	857.83	992.00	931.00	2422.00	799.00	2091.83	2100.92	834.83	3420.25	4018.67	1819.50	242.00	612.92	635.33	546.58	1678.50

NUMBER OF TAXA	U/Gv Bere	U/Gv Cerne	U/Gv Lewell	U/Gv Lo Piddle	U/Gv Mid Piddle	U/Gv Tadnoll	U/Ra Bere	U/Ra Cerne	U/Ra Lewell	U/Ra Lo Piddle	U/Ra Mid Piddle	U/Ra Tadnoll	U/Re Bere	U/Re Cerne	U/Re Lewell	U/Re Lo Piddle	U/Re Tadnoll
COLEOPTERA	3	4	4	6	2	3	2	4	2	3	2	3	5	2	2	5	2
CRUSTACEA	2	3	3	3	2	2	2	2	2	2	2	2	2	3	3	3	3
DIPTERA	6	6	4	6	5	4	4	4	3	4	4	4	4	5	6	7	5
EPHEMEROPTERA	5	6	4	6	6	5	4	6	2	4	6	4	3	5	3	5	2
FISH	1	0	0	1	0	11	1	1	0	3	1	1	0	0	0	3	1
HEMIPTERA	0	1	0	0	0	0	1	1	0	1	0	0	3	3	2	3	0
HIRUDINEA	3	4	1	1	1	0	0	0	1	3	0	0	0	1	1	4	0
MOLLUSCA	2	4	4	5	6	3	2	3	3	6	4	1	3	4	3	11	4
ODONATA	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0
OTHER	3	3	3	3	3	3	1	3	2	1	2	2	1	4	3	3	3
PLECOPTERA	1	1	0	4	1	3	0	0	0	1	0	0	0	0	0	1	0
TRICHOPTERA	4	7	13	13	13	8	1	7	2	11	6	8	1	7	8	10	5
TOTAL	30	38	36	46	39	42	16	30	17	38	27	25	22	33	32	55	25

MAY

ABUNDANCE	U/A Bere	U/A Cerne	U/A Lo Piddle	U/A Mid Piddle	U/OH Bere	U/OH Cerne	U/OH Lewell	U/OH Lo Piddle	U/OH Mid Piddle	U/OH Tadnoll	U/M Bere	U/M Cerne	U/M Lewell	U/M Lo Piddle	U/M Mid Piddle	U/M Tadnoll
COLEOPTERA	17.00	8.50	11.67	5.83	16.17	15.17	9.00	102.50	20.50	39.17	9.33	15.31	14.42	35.88	13.17	20.83
HEMIPTERA	14.33	11.58	15.50	37.83	2.00	4.67	0.00	5.33	24.83	0.00	11.56	19.44	1.25	10.54	31.33	0.00
TRICHOPTERA	22.58	30.67	77.83	43.83	11.83	57.75	53.33	692.33	37.83	29.50	14.28	37.94	113.50	257.00	40.83	20.83
CRUSTACEA	18.42	114.83	9.67	22.00	42.83	84.83	54.17	159.50	30.33	78.00	16.19	71.31	61.75	61.00	26.17	50.92
DIPTERA	14.83	65.50	29.17	40.00	46.83	214.83	199.67	903.83	585.17	442.33	20.97	347.81	158.50	275.46	312.58	360.00
FISH	0.67	0.17	0.33	0.33	0.00	0.17	0.00	0.33	0.33	2.83	0.67	0.17	0.00	1.04	0.33	1.58
HIRUDINEA	0.17	6.08	0.67	0.67	0.67	0.33	0.00	10.83	0.00	0.00	0.17	1.00	1.08	4.46	0.33	0.00
EPHEMEROPTERA	240.17	238.67	118.83	77.17	236.17	335.17	100.00	846.33	237.50	401.00	216.67	239.86	156.17	310.13	157.33	278.50
MOLLUSCA	23.67	124.67	39.33	244.50	24.83	16.83	3.17	18.50	90.00	46.83	14.06	93.36	6.92	60.58	167.25	43.58
ODONATA	1.25	1.75	10.67	6.33	0.00	3.17	6.50	15.67	1.00	0.00	1.14	1.33	3.75	15.67	3.67	0.00
OTHER	11.33	383.50	2.50	26.17	6.50	36.25	56.33	35.00	58.50	158.83	11.69	103.61	71.50	18.04	42.33	662.25
PLECTOPTERA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.63	0.00	0.00
TOTAL	364.42	985.92	316.17	504.67	387.83	769.17	482.17	2792.33	1086.00	1198.50	316.72	931.14	588.83	1050.42	795.33	1438.50

NUMBER OF TAXA	U/A Bere	U/A Cerne	U/A Lo Piddle	U/A Mid Piddle	U/OH Bere	U/OH Cerne	U/OH Lewell	U/OH Lo Piddle	U/OH Mid Piddle	U/OH Tadnoll	U/M Bere	U/M Cerne	U/M Lewell	U/M Lo Piddle	U/M Mid Piddle	U/M Tadnoll
COLEOPTERA	6	5	6	7	3	5	3	6	4	4	5	4	3	5	6	3
CRUSTACEA	2	3	3	3	3	3	2	2	2	3	1	2	3	3	3	3
DIPTERA	3	7	5	4	7	6	4	5	4	8	4	5	5	6	4	7
EPHEMEROPTERA	4	7	3	7	4	7	2	7	6	6	3	6	3	5	7	4
FISH	1	1	1	1	0	1	0	1	1	1	1	1	0	3	2	1
HEMIPTERA	5	5	5	4	4	2	0	3	3	0	5	3	1	4	4	0
HIRUDINEA	1	3	2	2	1	1	0	1	0	0	1	3	1	4	2	0
MOLLUSCA	5	5	8	9	5	5	3	6	10	4	4	7	3	9	10	4
ODONATA	1	1	1	1	0	1	1	1	2	0	1	2	1	1	2	0
OTHER	3	3	1	4	3	4	3	2	3	3	3	5	3	3	4	3
PLECOPTERA	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
TRICHOPTERA	2	7	7	9	3	8	3	17	7	7	2	7	6	11	8	6
TOTAL	31	46	42	51	33	41	21	52	42	36	29	47	27	54	50	31

MAY

ABUNDANCE	W/Gv	W/Gv	W/Gv	W/OH	W/OH	W/OH
	Bere	Mid Piddle	Tadnoll	Bere	Mid Piddle	Tadnoll
COLEOPTERA	76.17	67.17	104.00	13.33	9.67	17.17
HEMIPTERA	0.00	0.00	0.00	7.17	4.33	5.67
TRICHOPTERA	46.50	30.33	20.83	16.50	23.67	39.83
CRUSTACEA	2.17	93.17	34.67	13.00	54.83	15.17
DIPTERA	50.83	230.00	80.50	98.83	479.50	159.17
FISH	0.00	0.00	0.33	0.00	1.00	0.00
HIRUDINEA	2.83	8.00	0.00	2.17	0.00	2.17
EPHEMEROPTERA	163.17	542.00	44.00	192.83	232.83	36.83
MOLLUSCA	30.33	25.17	23.67	154.50	7.67	26.00
ODONATA	0.00	0.00	0.33	0.33	0.00	0.33
OTHER	8.67	122.67	23.83	26.00	36.83	147.33
PLECTOPTERA	0.00	2.17	45.50	0.00	0.00	2.50
TOTAL	380.67	1120.67	377.67	524.67	850.33	452.17

NUMBER OF TAXA	W/Gv	W/Gv	W/Gv	W/OH	W/OH	W/OH
	Bere	Mid Piddle	Tadnoll	Bere	Mid Piddle	Tadnoll
COLEOPTERA	3	2	3	4	5	3
CRUSTACEA	1	2	2	2	3	2
DIPTERA	7	4	4	6	4	6
EPHEMEROPTERA	6	6	5	4	7	2
FISH	0	0	1	0	1	0
HEMIPTERA	0	0	0	0	1	2
HIRUDINEA	2	2	0	1	0	1
MOLLUSCA	2	5	2	5	6	4
ODONATA	0	0	1	1	0	1
OTHER	1	3	1	2	2	3
PLECOPTERA	0	1	2	0	0	2
TRICHOPTERA	7	6	9	8	7	5
TOTAL	29	31	30	33	36	31

JULY

ABUNDANCE	G/Gv	G/Gv	G/Gv	G/Gv	G/Gv	G/Ra	G/Ra	G/Ra	G/Ra	G/Ra	G/GA	G/GA	G/GA	G/GA	G/GA
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle
COLEOPTERA	67.50	61.17	28.50	20.50	7.17	14.33	2.17	6.50	25.17	33.50	11.33	36.50	78.83	112.17	123.67
CRUSTACEA	17.67	622.17	54.33	171.83	41.50	4.67	186.33	87.00	45.83	316.33	20.50	440.00	275.17	110.50	97.00
DIPTERA	868.33	140.00	69.33	59.83	145.17	1211.17	810.33	60.67	340.17	455.67	400.33	61.00	76.17	154.50	116.17
EPHEMEROPTERA	386.00	286.67	45.50	57.00	91.67	1027.33	543.83	801.67	606.67	416.00	209.00	268.08	253.50	281.67	24.17
FISH	0.00	2.17	0.00	0.67	0.00	2.83	0.00	0.67	3.00	3.50	2.50	2.67	15.33	58.50	11.17
HEMIPTERA	0.00	0.00	0.33	0.00	4.33	0.00	0.00	0.00	0.00	2.83	6.83	147.25	60.83	257.33	350.50
HIRUDINEA	23.67	25.17	14.00	10.00	0.67	0.00	0.00	34.50	2.50	21.50	15.17	3.00	14.00	0.33	1.00
MOLLUSCA	26.33	80.83	31.67	2.50	166.00	0.00	14.00	150.00	22.33	94.50	32.00	523.42	172.00	58.33	202.83
ODONATA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.67	0.00	0.00	0.00	2.17	0.67
OTHER	58.83	67.17	216.67	10.83	21.67	39.00	3.83	32.50	108.33	49.83	24.50	23.83	39.00	0.00	7.17
PLECOPTERA	8.67	0.00	0.00	25.17	0.00	0.00	0.00	0.00	2.17	0.33	0.00	0.17	0.00	0.00	0.00
TRICHOPTERA	27.17	15.17	45.67	18.50	23.00	6.83	0.00	51.33	76.67	78.17	15.83	6.25	25.50	56.33	54.33
TOTAL	1484.17	1300.50	506.00	376.83	501.17	2306.17	1560.50	1227.00	1232.83	1472.83	738.00	1512.17	1010.33	1091.83	988.67

NUMBER OF TAXA	G/Gv	G/Gv	G/Gv	G/Gv	G/Gv	G/Ra	G/Ra	G/Ra	G/Ra	G/Ra	G/GA	G/GA	G/GA	G/GA	G/GA
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle
COLEOPTERA	4	5	3	4	4	5	1	2	5	4	8	12	8	7	6
CRUSTACEA	2	3	3	2	3	2	2	3	1	3	3	3	4	4	3
DIPTERA	7	4	1	3	2	5	2	2	3	5	9	8	4	7	5
EPHEMEROPTERA	7	3	3	4	5	4	2	2	2	4	3	4	2	4	3
FISH	0	1	0	1	0	2	0	1	1	1	1	3	3	4	2
HEMIPTERA	0	0	1	0	1	0	0	0	0	2	1	7	7	9	7
HIRUDINEA	3	3	3	3	2	0	0	4	2	3	2	4	4	1	1
MOLLUSCA	4	5	7	2	3	0	2	7	7	9	5	11	11	10	12
ODONATA	0	0	0	0	0	0	0	2	0	2	0	0	0	1	2
OTHER	5	2	3	3	2	2	1	2	1	3	3	4	3	0	1
PLECTOPTERA	1	0	0	2	0	0	0	0	1	1	0	1	0	0	0
TRICHOPTERA	4	5	6	9	6	3	0	10	15	11	2	4	3	3	2
TOTAL	37	31	30	33	28	23	10	35	38	48	37	61	49	50	44

JULY

ABUNDANCE	U/Gv Bere	U/Gv Cerne	U/Gv Lewell	U/Gv Lo Pid	U/Gv Mid Pid	U/Gv Tadnoll	U/Ra Bere	U/Ra Cerne	U/Ra Lo Pid	U/Ra Tadnoll	U/Re Cerne	U/Re Lo Pid	U/Re Mid Pid	U/Re Tadnoll
COLEOPTERA	63.58	114.58	69.67	138.33	85.17	98.17	16.00	6.67	18.17	28.50	5.58	23.83	11.00	25.50
CRUSTACEA	53.00	321.00	197.17	131.25	97.83	123.50	9.75	71.58	46.50	132.67	187.58	186.33	20.17	175.50
DIPTERA	202.75	87.92	58.50	196.67	581.67	121.33	2037.17	1639.25	1745.25	747.83	193.92	373.33	331.50	458.17
EPHEMEROPTERA	102.33	258.83	45.50	223.08	38.50	69.33	749.83	622.00	600.17	218.83	170.08	136.50	13.00	138.67
FISH	1.08	0.33	0.33	1.58	2.17	0.33	1.58	0.17	2.50	0.67	0.00	2.83	0.00	0.33
HEMIPTERA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.92	0.00	11.00	20.17	8.50	11.17
HIRUDINEA	10.33	14.75	2.50	2.50	9.67	2.17	1.25	1.08	0.33	4.33	9.92	5.67	0.00	8.67
MOLLUSCA	208.25	191.00	4.67	9.42	343.00	55.83	13.58	17.83	12.33	54.50	129.25	74.50	32.50	69.33
ODONATA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	4.42	4.17	0.00	0.00
OTHER	36.25	28.25	179.83	97.50	229.67	4.67	33.75	20.58	114.83	28.17	37.00	30.33	28.17	17.67
PLECOPTERA	5.92	4.67	0.00	28.25	0.33	19.00	1.25	0.17	1.08	10.83	0.17	0.00	0.00	9.00
TRICHOPTERA	15.83	28.75	47.17	132.75	193.83	28.00	2.17	4.75	86.00	61.33	7.67	87.83	29.33	31.00
TOTAL	699.33	1050.08	605.33	961.33	1581.83	522.33	2866.33	2384.08	2635.75	1287.67	756.58	945.50	475.83	945.00

NUMBER OF TAXA	U/Gv Bere	U/Gv Cerne	U/Gv Lewell	U/Gv Lo Pid	U/Gv Mid Pid	U/Gv Tadnoll	U/Ra Bere	U/Ra Cerne	U/Ra Lo Pid	U/Ra Tadnoll	U/Re Cerne	U/Re Lo Pid	U/Re Mid Pid	U/Re Tadnoll
COLEOPTERA	4	5	4	4	7	2	3	3	3	3	3	9	5	7
CRUSTACEA	3	4	4	3	3	2	2	2	2	2	3	3	3	3
DIPTERA	6	4	1	7	7	4	6	3	4	6	7	7	3	8
EPHEMEROPTERA	6	4	3	4	5	3	4	3	3	3	3	2	3	5
FISH	1	1	1	1	1	1	1	1	1	1	0	2	1	1
HEMIPTERA	0	0	0	0	0	0	0	0	2	0	2	4	4	3
HIRUDINEA	3	2	1	2	3	1	1	1	1	1	4	3	0	2
MOLLUSCA	6	5	3	4	6	4	5	4	5	5	5	10	9	7
ODONATA	0	0	0	0	0	0	0	0	1	0	1	1	0	0
OTHER	3	3	2	2	2	2	2	2	1	3	4	3	2	4
PLECTOPTERA	2	1	0	2	1	2	1	1	1	2	1	0	0	2
TRICHOPTERA	5	7	6	8	13	7	1	5	7	3	5	11	6	7
TOTAL	37	35	25	36	48	28	24	22	29	29	35	55	36	49

JULY

ABUNDANCE	U/A Bere	U/A Cerne	U/OH Bere	U/OH Cerne	U/OH Lo Pid	U/OH Mid Pid	U/OH Tadnoll	U/M Bere	U/M Cerne	U/M Lo Pid	U/M Mid Pid	U/M Tadnoll
COLEOPTERA	10.00	30.25	35.17	14.92	37.67	41.67	96.83	22.58	16.92	30.75	26.33	61.17
CRUSTACEA	7.50	192.42	147.33	102.00	132.50	62.83	182.00	77.42	160.67	159.42	41.50	178.75
DIPTERA	223.17	100.92	392.17	418.33	243.33	197.17	542.00	307.67	237.72	308.33	264.33	500.08
EPHEMEROPTERA	182.00	156.33	230.00	218.83	181.25	48.00	114.83	206.00	181.75	158.88	30.50	126.75
FISH	4.67	0.00	2.33	0.00	2.92	10.83	1.67	3.50	0.00	2.88	5.42	1.00
HEMIPTERA	5.00	19.42	15.83	5.42	26.25	89.50	9.00	10.42	11.94	23.21	49.00	10.08
HIRUDINEA	2.17	10.42	6.33	1.58	2.50	2.17	2.17	4.25	7.31	4.08	1.08	5.42
MOLLUSCA	90.83	121.83	97.33	13.58	92.83	130.17	53.00	94.08	88.22	83.67	81.33	61.17
ODONATA	0.00	3.25	0.33	1.58	6.92	2.50	0.00	0.17	3.08	5.54	1.25	0.00
OTHER	19.83	120.42	34.67	17.83	7.75	13.33	28.17	27.25	58.42	19.04	20.75	22.92
PLECOPTERA	0.00	0.17	2.17	0.17	1.08	0.00	7.17	1.08	0.17	0.54	0.00	8.08
TRICHOPTERA	3.50	3.67	12.83	9.33	47.83	54.83	41.17	8.17	6.89	67.83	42.08	36.08
TOTAL	548.67	759.08	976.50	803.58	784.11	655.17	1078.00	762.58	773.08	864.81	565.50	1011.50

NUMBER OF TAXA	U/A Bere	U/A Cerne	U/OH Bere	U/OH Cerne	U/OH Lo Pid	U/OH Mid Pid	U/OH Tadnoll	U/M Bere	U/M Cerne	U/M Lo Pid	U/M Mid Pid	U/M Tadnoll
COLEOPTERA	6	6	10	3	7	8	7	8	4	8	7	7
CRUSTACEA	1	3	2	4	3	2	3	2	3	3	3	3
DIPTERA	0	0	5	6	9	6	8	4	4	8	5	8
EPHEMEROPTERA	3	4	4	3	3	4	5	4	3	3	4	5
FISH	2	0	3	0	3	3	1	3	0	3	2	1
HEMIPTERA	3	2	4	2	5	5	2	4	2	4	5	3
HIRUDINEA	1	2	2	2	2	1	1	2	3	2	1	2
MOLLUSCA	6	4	6	4	8	10	7	6	4	9	10	7
ODONATA	0	1	1	1	1	2	0	1	1	1	1	0
OTHER	3	3	3	4	2	3	3	3	3	3	3	4
PLECTOPTERA	0	1	1	1	1	0	1	1	1	0	0	2
TRICHOPTERA	2	4	1	5	10	8	8	2	4	11	7	8
TOTAL	32	31	42	32	52	52	46	37	33	53	44	48

JULY

ABUNDANCE	W/Gv Bere	W/Gv Mid Pid	W/Gv Tadnoll	W/OH Bere	W/OH Mid Pid	W/OH Tadnoll
COLEOPTERA	73.67	80.83	169.33	8.50	27.00	35.50
CRUSTACEA	8.50	158.83	149.83	30.67	56.33	138.67
DIPTERA	128.83	95.83	75.83	214.67	223.17	126.67
EPHEMEROPTERA	62.00	7.00	32.50	58.83	2.50	32.83
FISH	0.00	0.33	0.00	0.33	2.17	0.00
HEMIPTERA	0.00	0.00	0.00	3.83	9.67	9.33
HIRUDINEA	6.33	5.00	4.33	2.50	2.50	4.33
MOLLUSCA	45.50	13.67	117.00	50.33	42.67	185.17
ODONATA	0.00	0.00	0.00	4.33	0.00	0.00
OTHER	65.00	125.50	67.17	13.33	11.17	80.17
PLECOPTERA	7.83	6.67	79.33	0.00	0.00	4.67
TRICHOPTERA	295.17	1204.83	49.33	3.50	64.17	66.50
TOTAL	692.83	1698.50	744.67	390.83	441.33	683.83

NUMBER OF TAXA	W/Gv Bere	W/Gv Mid Pid	W/Gv Tadnoll	W/OH Bere	W/OH Mid Pid	W/OH Tadnoll
COLEOPTERA	2	2	3	4	7	8
CRUSTACEA	2	2	3	3	2	3
DIPTERA	5	4	4	9	6	5
EPHEMEROPTERA	5	5	3	4	1	3
FISH	0	1	0	1	1	0
HEMIPTERA	0	0	0	2	1	4
HIRUDINEA	2	1	1	1	1	2
MOLLUSCA	3	4	3	8	7	8
ODONATA	0	0	0	1	0	0
OTHER	3	4	2	2	3	2
PLECTOPTERA	1	1	2	0	0	1
TRICHOPTERA	4	7	8	2	6	8
TOTAL	27	31	29	37	35	44

SEPTEMBER

ABUNDANCE	G/Gv Bere	G/Gv Cerne	G/Gv Lewell	G/Gv Lo Piddle	G/Gv Mid Piddle	G/Ra Bere	G/Ra Cerne	G/Ra Lewell	G/Ra Lo Piddle	G/M Bere	G/M Cerne	G/M Lewell	G/M Lo Piddle	G/M Mid Piddle
COLEOPTERA	82.67	51.00	0.67	60.83	79.00	32.67	2.17	0.00	7.17	31.33	4.33	50.67	36.33	9.00
HEMIPTERA	0.00	0.00	0.00	12.17	0.00	0.00	0.00	0.00	0.00	38.00	13.50	47.83	342.83	74.00
TRICHOPTERA	36.83	31.83	7.67	82.50	52.50	2.50	44.67	4.67	44.50	11.17	11.50	11.50	20.17	15.17
CRUSTACEA	18.00	286.33	65.83	175.83	71.50	11.83	262.50	20.17	67.17	25.67	696.50	114.00	102.17	42.00
DIPTERA	1404.50	70.00	20.83	447.33	352.33	1205.67	264.33	447.00	842.67	297.83	122.00	477.67	216.17	461.83
FISH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	5.00	5.33	0.33	2.50	8.83	2.67
HIRUDINEA	32.50	31.33	18.67	53.33	4.67	85.00	13.00	0.00	15.17	24.50	13.00	15.50	58.50	3.17
EPHEMEROPTERA	244.83	151.00	31.67	178.67	45.83	210.17	1930.50	189.17	496.17	41.83	393.50	81.67	99.67	24.17
MOLLUSCA	15.17	80.83	9.00	19.83	1331.67	7.17	339.00	48.33	27.83	36.67	164.17	1224.33	692.50	314.00
ODONATA	0.00	2.17	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	2.17	0.00	2.17	0.00
OTHER	60.67	288.17	353.17	61.00	71.50	69.33	169.00	8.67	99.67	69.33	8.67	23.83	47.67	52.00
PLECOPTERA	0.33	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.33	0.00
TOTAL	1895.50	992.67	507.83	1091.83	2009.00	1624.33	3025.17	718.33	1607.50	582.00	1429.67	2049.50	1627.33	998.00

NUMBER OF TAXA	G/Gv Bere	G/Gv Cerne	G/Gv Lewell	G/Gv Lo Piddle	G/Gv Mid Piddle	G/Ra Bere	G/Ra Cerne	G/Ra Lewell	G/Ra Lo Piddle	G/M Bere	G/M Cerne	G/M Lewell	G/M Lo Piddle	G/M Mid Piddle
COLEOPTERA	3	3	2	6	5	3	1	0	3	8	2	12	7	4
CRSUTACEA	2	2	2	2	1	2	2	2	1	3	2	3	2	3
DIPTERA	10	4	4	9	8	7	3	3	3	9	4	8	6	5
EPHEMEROPTERA	5	4	4	5	2	4	4	1	2	6	3	3	4	8
FISH	1	0	0	1	1	1	1	2	2	2	2	1	3	2
HEMIPTERA	0	0	0	2	0	0	0	0	0	5	3	7	5	5
HIRUDINEA	3	3	2	3	2	3	3	0	3	4	2	4	2	2
MOLLUSCA	5	6	2	4	3	4	7	6	7	6	5	11	10	9
ODONATA	0	1	0	0	0	0	0	0	1	0	1	0	1	0
OTHER	2	3	1	3	2	2	2	2	1	3	2	3	3	3
PLECOPTERA	1	0	1	1	0	0	0	0	0	1	0	0	1	0
TRICHOPTERA	4	8	2	8	8	2	8	2	6	5	4	4	3	2
TOTAL	36	34	20	44	32	28	31	18	29	52	30	56	47	43

SEPTEMBER

ABUNDANCE	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Ra	U/Ra	U/Ra	U/Ra	U/Ra	U/M	U/M	U/M	U/M	U/M	U/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll
COLEOPTERA	171.67	196.58	87.00	372.33	362.50	100.00	38.50	45.67	28.50	129.25	118.33	47.22	40.25	42.33	76.83	10.83	49.00
HEMIPTERA	2.33	0.00	0.00	1.92	41.17	0.00	1.08	0.33	0.00	0.00	0.00	36.17	16.75	9.67	24.92	0.67	3.17
TRICHOPTERA	28.92	50.67	64.00	82.08	203.67	24.00	17.67	82.67	203.33	204.33	318.17	22.83	30.75	51.67	34.17	80.00	43.83
CRUSTACEA	85.50	338.17	228.50	128.17	275.17	290.67	74.83	195.17	158.17	238.08	884.00	171.83	295.92	249.83	155.92	152.00	541.67
DIPTERA	669.33	48.92	130.67	447.08	216.17	31.00	1096.50	236.50	184.83	3407.75	153.83	203.00	282.67	204.00	210.42	187.00	136.83
FISH	0.00	0.00	0.00	0.00	2.50	0.00	0.33	0.00	0.00	0.17	0.00	3.17	0.00	1.67	2.50	0.00	0.00
HIRUDINEA	8.50	8.83	9.50	5.83	7.17	2.50	16.42	9.67	2.17	4.50	9.00	20.89	13.75	17.67	7.33	4.67	11.83
EPHEMEROPTERA	82.83	187.75	19.17	190.42	239.67	19.50	353.17	943.17	394.33	593.83	260.00	86.72	147.50	13.67	89.08	1054.00	37.50
MOLLUSCA	166.92	30.50	15.17	46.08	65.67	67.17	206.58	639.50	140.00	275.67	260.00	387.61	220.75	68.00	247.33	418.50	98.17
ODONATA	0.00	0.33	0.00	0.17	0.00	0.00	1.58	19.42	2.17	1.92	3.17	0.67	7.75	1.33	11.92	19.83	2.50
OTHER	104.58	55.58	147.67	127.83	260.33	23.83	189.58	53.25	22.33	120.25	113.33	249.61	22.92	4.33	15.17	39.33	6.50
PLECOPTERA	0.83	0.33	0.00	15.50	5.00	8.67	0.00	0.33	0.00	1.08	11.83	1.56	0.17	0.00	5.42	0.33	9.00
TOTAL	1321.42	917.67	701.67	1417.42	1679.00	567.33	1996.25	2225.67	1135.83	4976.83	2131.67	1231.28	1079.17	664.17	881.00	1967.17	940.00

DIVERSITY	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Ra	U/Ra	U/Ra	U/Ra	U/Ra	U/M	U/M	U/M	U/M	U/M	U/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll
COLEOPTERA	5	4	4	7	6	4	6	3	1	5	3	9	4	6	9	2	6
CRSUTACEA	3	3	3	3	2	2	3	3	3	2	3	2	3	2	3	3	3
DIPTERA	7	6	6	9	9	2	4	5	3	3	5	7	9	6	8	3	9
EPHEMEROPTERA	6	5	6	5	6	3	4	9	4	4	3	3	6	3	3	10	3
FISH	1	1	0	1	1	1	2	1	0	2	1	2	0	2	1	1	1
HEMIPTERA	1	0	0	1	1	0	1	1	0	0	0	4	4	3	6	2	3
HIRUDINEA	4	3	4	3	2	2	4	3	1	2	2	3	4	3	3	2	3
MOLLUSCA	6	4	4	7	8	3	6	6	6	11	7	8	7	5	11	7	7
ODONATA	0	1	0	1	0	0	1	2	1	1	1	1	1	1	2	1	2
OTHER	3	3	3	3	4	3	3	3	3	2	3	4	2	1	2	3	3
PLECOPTERA	1	1	0	1	1	1	0	1	0	1	3	1	1	0	1	1	2
TRICHOPTERA	4	8	8	14	11	7	3	9	6	10	14	4	6	7	8	7	13
TOTAL	38	36	38	53	51	28	34	43	28	40	45	46	45	39	54	42	55

SEPTEMBER

ABUNDANCE	W/Gv	W/Gv	W/Gv	W/OH	W/OH	W/OH
	Bere	Mid Piddle	Tadnoll	Bere	Mid Piddle	Tadnoll
COLEOPTERA	305.50	257.00	214.83	75.33	11.25	66.00
HEMIPTERA	0.00	0.00	0.00	11.83	0.50	3.25
TRICHOPTERA	175.00	1010.33	43.17	50.50	97.50	27.00
CRUSTACEA	15.83	448.50	106.17	63.33	71.50	250.75
DIPTERA	43.17	52.00	15.83	94.00	74.75	109.75
FISH	0.00	0.00	0.00	0.00	1.00	0.00
HIRUDINEA	7.83	10.67	2.17	27.33	7.00	7.00
EPHEMEROPTERA	53.67	352.33	26.00	50.67	35.75	71.50
MOLLUSCA	49.83	6.83	23.83	85.33	65.25	127.25
ODONATA	0.00	0.00	0.00	7.33	0.00	0.50
OTHER	74.50	131.00	48.00	55.00	39.00	3.75
PLECOPTERA	7.50	0.33	13.33	2.67	0.50	22.75
TOTAL	732.83	2269.00	493.33	523.33	404.00	689.50

DIVERSITY	W/Gv	W/Gv	W/Gv	W/Ra	W/Ra	W/Ra
	Bere	Mid Piddle	Tadnoll	Bere	Mid Piddle	Tadnoll
COLEOPTERA	4	4	4	11	4	6
CRSUTACEA	2	2	2	2	2	3
DIPTERA	5	4	3	10	2	5
EPHEMEROPTERA	5	7	2	5	5	2
FISH	0	0	1	1	3	1
HEMIPTERA	0	0	0	4	1	1
HIRUDINEA	3	1	1	3	1	3
MOLLUSCA	3	1	3	8	6	7
ODONATA	0	0	0	2	0	1
OTHER	3	4	3	5	3	2
PLECOPTERA	1	1	2	1	1	2
TRICHOPTERA	7	8	8	8	8	6
TOTAL	33	32	29	60	36	39

JANUARY

ABUNDANCE	G/Gv	G/Gv	G/Gv	G/Gv	G/Gv	G/Ra	G/Ra	G/Ra	G/Ra	G/M	G/M	G/M	G/M	G/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle
COLEOPTERA	69.33	27.67	21.17	16.17	10.00	0.00	2.83	0.33	0.33	3.83	31.33	2.83	3.17	30.67
CRUSTACEA	60.67	698.00	208.00	216.67	67.50	0.33	94.50	32.00	0.00	96.67	871.00	37.83	50.00	79.67
DIPTERA	189.83	50.33	180.33	125.67	22.33	2033.00	559.33	358.17	2857.83	166.50	212.67	80.50	167.83	245.17
EPHEMEREPTERA	201.83	54.50	57.33	86.00	130.50	0.67	51.17	27.00	5.00	16.50	42.17	5.00	11.17	95.33
FISH	0.33	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.33	1.33	0.67	9.17	0.00	28.33
HEMIPTERA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.83	8.67	2.50	56.83	28.17
HIRUDINEA	64.17	13.33	26.17	13.17	5.67	4.33	0.00	0.33	0.00	4.50	8.67	3.17	2.50	9.67
MOLLUSCA	10.33	100.50	17.83	12.67	392.50	1.00	185.17	13.33	0.00	95.33	460.17	46.67	78.17	437.00
ODONATA	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	2.17	3.17	0.33	0.00	0.00
OTHER	152.00	69.50	260.67	75.83	26.00	0.00	0.67	0.33	2.17	65.33	112.67	39.33	24.17	4.33
PLECOPTERA	0.00	0.00	0.00	6.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRICHOPTERA	58.33	94.50	46.50	82.50	17.17	5.67	25.83	8.00	0.00	483.17	282.00	100.17	1045.67	306.83
TOTAL	867.50	1817.50	1026.33	852.17	739.17	2045.33	1025.17	471.50	2865.67	1044.50	3004.17	376.50	1496.33	1420.67

NUMBER OF TAXA	G/Gv	G/Gv	G/Gv	G/Gv	G/Gv	G/Ra	G/Ra	G/Ra	G/Ra	G/M	G/M	G/M	G/M	G/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Bere	Cerne	Lewell	Lo Piddle	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle
COLEOPTERA	4	4	3	4	4	0	2	1	1	4	4	2	3	7
CRUSTACEA	2	3	3	2	2	1	3	2	0	3	3	3	4	3
DIPTERA	10	6	8	7	4	3	3	3	2	10	7	5	7	6
EPHEMEROPTERA	6	9	6	6	6	1	3	4	2	3	4	3	3	4
FISH	1	0	0	1	0	0	0	0	1	1	2	2	0	3
HEMIPTERA	0	0	0	0	0	0	0	0	0	3	1	2	3	3
HIRUDINEA	3	3	3	3	2	2	0	1	0	4	2	2	2	3
MOLLUSCA	5	8	5	8	4	1	3	3	0	7	8	7	8	10
ODONATA	0	0	0	0	0	0	1	0	0	1	2	1	0	0
OTHER	4	3	3	2	4	0	1	1	1	3	3	2	3	1
PLECOPTERA	0	0	0	1	0	0	0	0	0	0	0	0	0	0
TERRESTRIAL	0	2	0	0	0	0	0	0	0	4	5	0	2	0
TRICHOPTERA	7	12	16	8	8	4	10	4	0	7	9	6	9	9
TOTAL	42	50	47	42	34	12	26	19	7	50	50	35	44	49

JANUARY

ABUNDANCE	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Ra	U/Ra	U/Ra	U/Ra	U/M	U/M	U/M	U/M	U/M	U/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll	Cerne	Lewell	Lo Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll
COLEOPTERA	70.75	90.33	51.50	297.75	29.83	11.50	5.67	4.33	21.08	0.33	27.83	41.92	8.17	39.92	25.50	30.00
CRUSTACEA	139.92	168.58	205.83	483.17	166.83	31.33	30.92	28.50	31.42	6.83	119.33	139.92	218.83	163.33	266.50	63.17
DIPTERA	47.33	129.58	91.00	112.42	17.50	90.17	129.25	745.50	1048.67	600.17	53.00	237.67	171.67	188.42	197.50	318.33
EPHEMEREPTERA	251.25	184.58	27.33	145.92	296.17	23.00	64.33	26.00	62.08	9.33	41.00	36.00	5.67	31.92	329.33	18.33
FISH	0.00	0.00	0.00	0.17	0.33	0.33	0.17	0.00	0.50	0.67	5.22	0.00	0.67	1.00	0.33	0.00
HEMIPTERA	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	31.89	0.67	2.83	6.33	22.33	0.33
HIRUDINEA	21.50	10.00	9.33	12.92	7.17	3.17	0.33	1.00	1.25	0.00	5.39	8.33	2.50	6.25	9.67	0.33
MOLLUSCA	248.25	39.83	31.00	63.75	129.17	8.17	31.83	5.00	218.00	3.17	152.83	95.58	37.17	131.75	777.33	58.83
ODONATA	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	2.28	6.08	2.83	17.08	5.00	0.00
OTHER	124.17	237.58	176.17	53.25	201.50	32.83	34.08	0.00	16.42	2.17	33.50	38.08	21.67	23.42	59.50	54.83
PLECOPTERA	0.00	0.00	0.00	3.58	0.00	0.00	0.00	0.00	0.50	0.00	0.00	1.08	0.00	0.00	0.00	2.50
TRICHOPTERA	31.17	78.33	79.33	139.08	97.83	33.17	89.33	13.67	154.50	20.33	121.94	146.00	316.17	838.42	301.83	101.17
TOTAL	1074.58	1111.00	877.33	1795.17	1113.17	265.00	420.67	852.50	1588.33	649.83	740.11	929.92	1025.33	1618.83	2300.67	729.00

NUMBER OF TAXA	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Gv	U/Ra	U/Ra	U/Ra	U/Ra	U/M	U/M	U/M	U/M	U/M	U/M
	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll	Cerne	Lewell	Lo Piddle	Tadnoll	Bere	Cerne	Lewell	Lo Piddle	Mid Piddle	Tadnoll
COLEOPTERA	3	6	3	7	5	2	3	1	5	1	8	6	2	8	6	6
CRUSTACEA	2	3	3	2	2	2	3	2	3	2	3	3	4	3	4	3
DIPTERA	6	9	3	10	5	3	5	2	3	1	13	14	9	9	6	7
EPHEMEROPTERA	6	9	6	6	8	2	7	1	6	3	5	7	3	5	7	3
FISH	0	0	0	1	1	1	1	0	1	1	2	0	2	1	1	0
HEMIPTERA	1	0	0	0	0	0	2	0	0	0	4	3	3	2	3	1
HIRUDINEA	3	3	3	5	3	2	1	1	2	0	4	4	2	2	3	1
MOLLUSCA	8	4	4	9	8	2	4	1	11	2	10	6	4	10	11	6
ODONATA	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0
OTHER	4	4	3	3	3	3	3	0	3	1	4	4	2	3	4	3
PLECOPTERA	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1
TERRESTRIAL	0	1	0	0	0	0	2	0	2	0	4	7	5	6	2	4
TRICHOPTERA	6	12	11	16	8	8	11	3	18	5	9	14	9	19	16	13
TOTAL	39	51	36	60	43	25	43	11	55	16	67	70	46	69	64	48

JANUARY

ABUNDANCE	W/Gv Bere	W/Gv Mid Piddle	W/Gv Tadnoll	W/OH Bere	W/OH Mid Piddle	W/OH Tadnoll
COLEOPTERA	151.67	158.50	188.83	14.00	20.00	38.25
CRUSTACEA	15.17	240.83	67.50	77.25	38.00	26.50
DIPTERA	61.50	41.67	15.50	83.25	83.25	78.50
EPHEMEREPTERA	108.83	252.67	25.83	33.50	29.75	10.25
FISH	0.00	0.67	0.00	0.00	1.50	2.00
HEMIPTERA	0.00	0.00	0.00	16.00	6.50	0.00
HIRUDINEA	8.17	16.67	2.50	4.25	6.50	0.50
MOLLUSCA	50.50	32.67	24.83	127.25	34.50	100.75
ODONATA	0.00	0.00	0.00	0.50	0.00	1.00
OTHER	90.17	135.00	27.00	39.00	104.50	23.25
PLECOPTERA	0.00	0.00	0.00	3.75	0.00	0.50
TRICHOPTERA	58.67	28.67	67.83	365.50	93.00	231.25
TOTAL	559.83	1152.50	487.33	864.25	476.25	546.75

NUMBER OF TAXA	W/Gv Bere	W/Gv Mid Piddle	W/Gv Tadnoll	W/Ra Bere	W/Ra Mid Piddle	W/Ra Tadnoll
COLEOPTERA	3	2	3	4	3	4
CRUSTACEA	2	3	2	3	2	2
DIPTERA	6	5	3	9	7	6
EPHEMEROPTERA	6	6	5	5	4	2
FISH	0	1	0	0	2	2
HEMIPTERA	0	0	0	3	1	0
HIRUDINEA	3	3	1	1	2	1
MOLLUSCA	4	6	4	5	7	4
ODONATA	0	0	0	1	0	1
OTHER	4	4	2	3	3	3
PLECOPTERA	0	0	0	2	0	1
TERRESTRIAL	0	1	0	2	6	2
TRICHOPTERA	9	5	13	10	9	11
TOTAL	37	36	33	48	46	39