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Benthic invertebrates in the headwaters of the Wye and Severn: effects of forestry and clear-felling

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Abstract

Invertebrate communities were recorded in three surveys between 1974 and 1994 of headwaters of the Wye and Severn at Plynlimon: the Afon Gwy (unforested), the Afon Hore (initially forested) and the Afon Hafren (forested throughout). The data cover periods before and after the clear-felling of a large area of coniferous forest in the catchment of the Hore.

All three streams contained invertebrates characteristic of acidic, upland conditions and had similar species richness. Differences in assemblage composition within streams between surveys could be related to differences in method or timing of sampling. All assemblages were dominated by Insecta, particularly Plecoptera and Diptera, whereas Ephemeroptera, Mollusca, Crustacea and some families of Trichoptera (notably Hydropsychidae and Philopotamidae) were poorly represented. The forested streams (Hafren and Hore) contained similar assemblages which differed from those in the unforested stream (Gwy) in containing lower densities of Ephemeroptera and Oligochaeta and much higher densities of nemourid and leuctrid Plecoptera.

Clear-felling of the Hore catchment resulted in changes in physical and chemical conditions (including a reduction of stream pH, and increases in dissolved aluminium concentration and summer water temperature) but no related change in the invertebrate assemblage. The apparent failure of invertebrates to respond as expected to substantial changes in local environmental conditions may reflect either a lack of understanding of causal links between invertebrates and environmental factors, or the over-riding influence of the dynamics of recruitment to populations.

Introduction

The Wye and the Severn, two of the major river systems of western Britain, have attracted the attention of many biologists and hydrologists. However, the invertebrate communities in their headwaters in the Plynlimon area have been largely neglected. Of the two rivers, the Wye is much the better known biologically (e.g. Edwards & Brooker, 1982; Ormerod & Edwards, 1987), but most previous studies have not sampled the headwaters above its confluence with the Afon Tarrenig (National Grid Reference SN 841827).

The relationships between land use (particularly forestry), water quality and stream communities have been well documented in Wales and other upland areas of the UK (e.g. Harriman & Morrison, 1982; Stoner *et al.*, 1984, Ormerod *et al.*, 1989). In poorly-buffered catchments, acid precipitation can lead to acidic conditions in the streams, combined with high concentrations of dissolved aluminium. These conditions frequently are associated with invertebrate assemblages that contain many Plecoptera and Diptera but few species of grazing invertebrates such as Ephemeroptera (Sutcliffe & Carrick, 1973; Townsend, Hildrew & Francis, 1983). Afforestation with conifers tends to exacerbate acidification leading to associations between forest cover and stream invertebrates (Harriman & Morrison, 1982, Stoner *et al.*, 1984). Much of the evidence linking water quality, afforestation and invertebrates comes from extensive surveys with small numbers of samples from many sites (e.g. Townsend, Hildrew & Francis, 1983; Ormerod & Edwards, 1987). There are few long term data sets and few studies of the response of invertebrate assemblages in UK streams to changes in water chemistry or to the extent of catchment afforestation.

In both the Wye and the Severn, the headwaters that drain south eastwards from the Plynlimon ridge provide freshwater ecologists with an extensive, upland study area with a long and detailed record of hydrology and water chemistry, a facility that is available in few other places in the UK. The differing land uses in the Wye (unforested) and Severn (mainly forested) subcatchments at Plynlimon invite comparison of the macroinvertebrate assemblages in their streams. Additionally, the controlled clear-felling in the Hore subcatchment has provided an opportunity to investigate the response of the macroinvertebrates to a marked environmental change.

This paper provides an overview based on three studies of invertebrates in the headwaters of the Wye and Severn.

Between them, they span three headwater streams (the Afon Gwy on the Wye, and the Afon Hore and Afon Hafren on the Severn), twenty years, three seasons, and periods before, during and after the clear-felling in the Hore. The paper aims to describe the invertebrate assemblages of the forested and unforested streams, and to summarise the changes that followed the removal of trees from a large proportion of the Hore subcatchment.

Methods

The earliest records of invertebrates in the Plynlimon streams are in unpublished reports by Gelsthorpe and Titmus (completed during industrial training placements at the National Museum of Wales, Cardiff) of a survey of the River Severn from its source to its confluence with the Afon Dulas near Llanidloes (SN 946839). Samples were obtained monthly (1974, February–April, Gelsthorpe: 1974, May to August, Titmus) by kick-sampling (2 minutes) in riffles, with net of 60 meshes/inch (pore size unknown but less than 420 μm, depending on thread diameter). Data from stations 9 and 10 (Fig. 1) in this study can be compared with the results of other surveys of the Plynlimon headwater streams. In addition, Gelsthorpe collected similar samples from the Hore (site 14) in February and March 1974.

Since 1988, sites in the Plynlimon area (Fig. 1) have been part of the long-term monitoring programme of the UK Acid Waters Monitoring Network. One site on the Gwy (UKAWMN site 17) has been sampled every April/May since 1988. A second site on the Hafren (UKAWMN site 18b) is a replacement for a site in the catchment of Llyn Brianne and has been sampled only since 1991. On each sampling occasion, three one-minute kick samples are collected. Further details of the sites and methods are available in UKAWMN (1991).

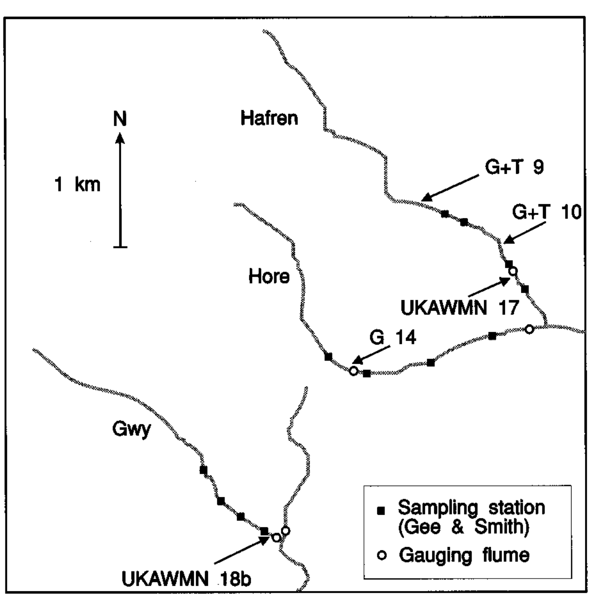

Fig. 1. *Study streams and sampling points (G, Gelsthorpe; T, Titmus; UKAWMN, United Kingdom Acid Waters Monitoring Network).*

The authors of the present paper surveyed macroinvertebrates in reaches of the Gwy, Hore and Hafren. In each reach, four stations (Fig. 1 & Table 1) were chosen to include similar microhabitats (a wide range of sizes of inorganic substrata, patches of moss, overhanging banks), but also to be as evenly spaced along the reach as possible. Macroinvertebrates were collected in July in every year from 1985 to 1991, and in October every year except 1987 and 1988. Various methods were used, but the data presented here derive from timed searches (2 minutes) of coarse substrata in riffles. Searching involved the disturbance of substrata by hand, including careful inspection of individual large particles, so that displaced invertebrates were carried downstream into a 250 μm pore size net. To compare invertebrate assemblages between the streams, and between pre- and post-felling periods within streams, data from 1985 and 1986 and from 1990 and 1991 have been pooled, as have records from the four stations on each stream. Further details are available in Gee & Smith (1995).

Results

SAMPLES FROM THE HAFREN AND HORE IN 1974

Gelsthorpe (unpublished) reported the abundance of taxa, whereas Titmus (unpublished) expressed representation as percentage values. Although total catches were also recorded by Titmus, in principle enabling conversion to absolute abundance, there are some irregularities in the values. Accordingly, the results of the two studies have been combined and presented here as percentages (Table 2).

Although the samples contained small numbers of individuals, particularly in July and August in the Hafren and in February and March in the Hore, they present a consistent picture of the invertebrate assemblages. Leuctrid stoneflies were abundant in both streams, except from May to August when both the species recorded have emerged and are on the wing. Emergence also accounts for the scarcity of *Amphinemura sulcicollis* in mid summer. *Siphonoperla torrentium* was frequent in spring but appeared to emerge in mid or late summer and was absent in August. *Protonemura meyeri*, which emerges in spring or early summer (Hynes, 1977), was present only in the samples in February and March.

In addition to the stoneflies, the samples were dominated by other insect groups, principally Diptera. Ephemeroptera were notable for their scarcity: the individuals recorded in May were *Siphlonurus lacustris*, but there is no record of the identity of the Ephemeroptera captured in July. Baetid mayfly larvae were captured regularly much further downstream (site 24, SN894847, and

Table 1. Location of sample stations.

Stream	National Grid Ref. (SN –)	Altitude (m)	Distance from source (km)
Gwy	818858	415	2.3
	819857	405	2.5
	820856	400	2.7
	823854	385	3.3
Hore	828871	435	1.8
	832869	395	2.2
	839871	355	2.9
	842872	345	3.4
Hafren	838883	385	2.7
	839883	380	2.9
	842879	355	3.4
	846874	340	4.0

Table 2. Percentage composition by taxon of kick samples from the Afon Hafren and Afon Hore. Only common genera and species are listed individually; rarer taxa are included in the totals of major groups. From unpublished data of A.J. Gelsthorpe and G. Titmus, collected in 1974.

	Sites 9 + 10 (Hafren)							Site 14 (Hore)	
Taxon	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Feb.	Mar.
Total Oligochaeta	1.2		0.3	0.6	1.2		1.0	2.8	
Total Acarina		0.4		1.1	2.1	2.8	2.8		
Total Ephemeroptera				0.2		1.5			
Protonemura meyeri	1.2	3.1						5.6	2.8
Amphinemura sulcicollis	2.3	6.3	3.4	6.8	6.5			11.1	7.0
Nemoura sp.									1.4
Leuctra sp.	12.8	10.5	3.9		3.1	4.2	6.7	52.8	15.5
Leuctra inermis	53.5	36.3	28.7	27.0	15.8			19.4	38.0
Leuctra nigra		0.4							
Capnia sp.	3.5		0.3						1.4
Isogenus nubecula			0.3						
Siphonoperla torrentium		2.3	2.0	3.9	12.1	2.8		2.8	5.6
Chloroperla tripunctata				0.9					
Total Plecoptera	73.3	59.0	38.5	39.8	37.5	8.4	9.6	91.7	71.8
Total Coleoptera				4.1	0.9	1.4	2.9		
Rhyacophila sp.			0.3						
Rhyacophila dorsalis		0.8	0.3	0.8	0.3				
Plectrocnemia conspersa				0.5			1.0		
Total Trichoptera		0.8	0.6	2.0	1.1	7.2	3.8		
Dicranota	11.6	0.8	0.6	0.6	0.6	1.5	6.7		2.8
Chironomidae	11.6	29.7	54.2	5.2	4.4	20.0	12.4	5.6	12.7
Simuliidae	2.3	7.0	5.9	0.2	4.7	14.4	17.2		12.7
Total Diptera	25.6	39.8	60.7	6.4	9.7	35.8	36.1	5.6	28.2
Total number of individuals	86	256	356	634	336	71	105	36	71

beyond) but apparently not within the area of the Hafren Forest. Trichoptera were represented mainly by Rhyacophilidae and Polycentropodidae. Overall, there is little to indicate any marked differences in the invertebrate assemblages of the Hafren and the Hore, although resolution is restricted by the short run of samples and the low numbers of specimens.

ACID WATERS MONITORING IN THE HAFREN AND GWY, 1988–94

Sampling in the Hafren started much earlier than in the Gwy, so to facilitate comparison Table 3 shows a summary of the entire Hafren data and also a subset which coincides in date with the Gwy samples.

These samples confirm the importance of leuctrid stoneflies, particularly *Leuctra inermis* which was the most numerous taxon in the Hafren in April/May. *Siphonoperla torrentium, Amphinemura sulcicollis* and *Brachyptera risi* were also abundant in both streams. Once again, Ephemeroptera were scarce, with only a single baetid being recorded from the Gwy. Trichoptera were represented mainly by rhyacophilids or polycentropodids, together with small numbers of some cased species.

All the abundant taxa were recorded in both streams, the greater total number of taxa in the Gwy being attributable mainly to very small numbers of specimens of taxa such as *Pisidium, Baetis, Capnia atra, Chloroperla tripunctata, Metalype fragilis* and *Oxyethira.* However, *Rhyacophila dorsalis* and *Oreodytes sanmarkii* were encountered frequently in the Hafren and were absent from the Gwy. Some taxa were disproportionately abundant in the Hafren. For instance, *Protonemura meyeri, Brachyptera risi, Leuctra inermis* and Tipulidae were much more abundant in the forested Hafren, even after allowing for the larger numbers of specimens in samples from this stream. These taxa contributed most to the much larger overall abundance of invertebrates in the Hafren.

Table 3. Abundances of invertebrates in kick samples collected from the Hafren and Gwy in April/May. Total numbers of taxa are minimum estimates allowing for possible overlap with undetermined specimens. Based on data provided by Ensis Ltd. and collected as part of the UK Acid Waters Monitoring Network.

	Hafren 1988–94	Gwy 1991–94	Hafren 1991–94
Pisidium sp.		1	
Oligochaeta	23	9	11
Baetis sp.		1	
Brachyptera risi	1046	26	966
Protonemura meyeri	84	3	38
Amphinemura sulcicollis	666	60	384
Nemoura sp.2		3	
Leuctra inermis	3402	218	2478
Leuctra hippopus	27	36	2
Leuctra nigra	4	2	1
Capnia atra		3	
Diura bicaudata	10	5	4
Isoperla grammatica	5	19	4
Siphonoperla torrentium	537	389	421
Chloroperla tripunctata	9	4	
Oreodytes sanmarkii	20		19
Ilybius ater	1		
Rhyacophila sp.	17	4	17
Rhyacophila dorsalis	69		44
Plectrocnemia sp.	32	17	23
Polycentropus sp.	1		1
Lype sp.	1		
Metalype fragilis		1	
Oxyethira sp.		1	
Limnephilidae undet.	4	4	4
Drusus annulatus	3		2
Ecclisopteryx guttulata	2		1
Potamophylax sp.	3	2	1
Tipulidae	334	6	325
Culicidae		5	
Chironomidae	205	390	144
Simuliidae	50	71	29
Empididae	10	4	9
Total number of individuals	6565	1284	4928
Total number of taxa	24	25	21

SAMPLES FROM THE GWY, HAFREN AND HORE IN 1985/6 AND 1990/1

Table 4 enables comparisons to be made between the invertebrate assemblages in the Gwy, Hafren and Hore in July and October, before and after the clear-felling of coniferous plantation in the Hore catchment.

Diptera and Plecoptera were numerous in all three streams in all samples, the former being disproportionately so in summer and the latter in autumn. Several species of Plecoptera were absent or scarce in July samples but abundant in October (*Protonemura meyeri, Amphinemura sulcicollis, Leuctra inermis, L. hippopus*), whereas *L. nigra, L. moselyi, Diura bicaudata* and *Siphonoperla torrentium* were encountered with similar frequency in both seasons. *Baetis vernus* (= *B. tenax*), the only ephemeropteran in these samples, was common in summer samples but scarce in autumn.

Despite the overall similarity of the macroinvertebrate assemblages in the streams, there were consistent differences between streams. Detailed statistical analysis will be presented elsewhere, but the following observations are significant to at least the 5% level. Oligochaeta were generally more abundant in the unforested Gwy than in the Hafren or Hore, particularly *Nais alpina* and *Lumbriculus variegatus.* The Gwy also yielded more specimens of *Baetis vernus* than either of the other streams in 1985/6 and

Table 4. Abundances of invertebrates in samples collected by timed searches at four sites in the Gwy, Hafren and Hore in July and October. Total numbers of taxa are minimum estimates allowing for possible overlap with undetermined specimens.

	Jul. 1985/6			Jul. 1990/1			Oct. 1985/6			Oct. 1990/1		
Taxon	Gwy	Hafren	Hore	Gwy	Hafren	Hore	Gwy	Hafren	Hore	Gwy	Hafren	Hore
Phagocata vitta (Dugès)	13	26	7	13	17	8	2	1	1	10	32	9
Crenobia alpina (Dana)	1						1	10	10			
Nais alpina Sperber	2			18	1		36	5		330	16	6
Tubificidae	4	1		1			1			2	1	1
Enchytraeidae	2	20	3	10	5	5	9	7		10		6
Lumbriculus variegatus (Müller)	1	1		17			3			7		
Stylodrilus heringianus Claparède	33	17	3	10	8	1	7	13	6	11	12	19
Baetis vernus Curtis	202	8	3	87	29	24	13			6	2	
Protonemura meyeri (Pictet)					2	1	1	264	58	1	331	160
Amphinemura sulcicollis (Stephens)	2	3	4		1			76	31	1	69	151
Leuctra inermis Kempny			37	1	2	16	6	451	58	13	979	1248
Leuctra hippopus (Kempny)			1	1		2	82	39	11	129	395	136
Leuctra nigra (Olivier)		5	2		5	2	6	55	110		9	19
Leuctra moselyi Morton	9	8	16	42	22	148	78	92	44	55	163	302
Diura bicaudata (Linné)	23	11	2	5	1	18	17	23	14	10	21	18
Siphonoperla torrentium (Pictet)	2	35	30		13	5	3			6	11	22
Chloroperlidae undet.			2				5	7	1			1
Oreodytes sanmarkii (Sahlberg)	2	2			4	1		3		1		
Dytiscidae (larvae)	1		1	2	7	6		1	2			
Rhyacophila dorsalis (Curtis)	12	5	1	12	3	5	18	76	15	16	94	35
Rhyacophila septentrionis McLachlan	1	5	1	2	15	27	1	1	1	2	6	
Rhyacophila obliterata McLachlan		21	2									
Rhyacophila undet.	2				3	1		32	2		1	1
Plectrocnemia conspersa (Curtis)	7	14	18	11	1	24	2	7	5	8	3	10
Plectrocnemia geniculata McLachlan			2	1		5	1	1	3			2
Polycentropus kingi McLachlan	1	2		6						3	1	
Limnephilidae undet.		1					1	19	4		28	5
Dicranota	12	15	10	43	24	15	35	60	38	28	49	25
Tipulidae	1	1			1		1	1		2	1	2
Chironomidae	460	489	39	599	1591	119	346	64	46	103	367	106
Simuliidae	554	168	26	802	912	449	16	51	44	43	58	141
Empididae	3	6	1	13	7	2	12	8		28	22	3
Total individuals	1350	864	211	1696	2674	884	703	1367	504	825	2671	2428
Total taxa	21	22	21	21	20	20	24	23	20	23	22	21

1990/1. Conversely, several species of Plecoptera (*Protonemura meyeri, Amphinemura sulcicollis, Leuctra inermis, L. nigra*) were much more abundant in the forested streams throughout the study. Abundances of Chironomidae and Simuliidae were generally lower in the Hore than in either the Gwy or the Hafren, and it is these differences that were mainly responsible for the lower overall abundance of invertebrates in the Hore in the summer samples. There was no evidence of any consistent difference in taxonomic richness between the forested and unforested streams.

In seeking evidence of changes in invertebrate assemblages consequent upon the clear-felling in the Hore catchment, attention focuses naturally first on species that initially differed in abundance between forested and unforested streams. *Baetis vernus* was much scarcer in the Hafren and Hore than in the Gwy before the felling, but increased in abundance post-felling. This increase occurred in both the felled and the unfelled stream so it cannot be attributed directly to clear-felling. The Plecoptera that were initially much more abundant in the forested streams did not decline in the Hore post-felling. In fact, the abundances of these species increased in the Hore (and relative to any changes in the Hafren) after the felling, and these changes were largely responsible for the marked increase in overall invertebrate abundance in the Hore.

Discussion

Whilst the three sets of invertebrate data available for the Plynlimon streams portray broadly similar assemblages, there are distinct differences between them. All the streams were dominated by Diptera and Plecoptera, and *Leuctra inermis* was the most common species of the latter. *Protonemura meyeri* was recorded in all the surveys, although this species was not detectable as larvae in summer, and *Leuctra nigra* was common to all as a minor element of the plecopteran fauna. *Leuctra hippopus* was not found by Gelsthorpe and Titmus, and was much less abundant in the UKAWMN samples than in the October samples of the authors' survey. This may reflect seasonal differences in the occurrence of larvae in stream sediments. Similarly, *Siphonoperla torrentium* was proportionately less abundant in the authors' samples than in the other studies. This may have been due to sampling later in the summer (Gelsthorpe and Titmus found highest densities in May and June). Kick-sampling may have been more effective than hand-sampling in dislodging this species from the interstices of the substratum. The invertebrate assemblages in the Plynlimon streams were broadly comparable with communities in other acidic, upland streams in Britain (e.g. Sutcliffe & Carrick, 1973; Harriman & Morrison, 1982; Wade *et al.*, 1989).

The numbers of *Brachyptera risi* differ strongly between the samples of the UKAWMN and those of Gelsthorpe, Titmus and the present authors. This cannot have been due to differences in the method or timing of sampling, since Gelsthorpe and Titmus sampled the Hafren at the same time of year and with a similar technique. As a separate exercise, additional samples were taken by the authors, using RIVPACS (Moss *et al.*, 1987) methodology (kick-sampling) in all three streams in May, July and October 1991. Although *B. risi* were found in these samples, they were represented by single individuals collected in the Hafren and Hore in May. The difference between UKAWMN results and those of the main survey of the present authors therefore is likely to be due both to the season of sampling, and to a recent increase in the abundance of *B. risi*. Most of the specimens of this species were collected in the UKAWMN in the period 1991–4 (Table 3), and there was an order of magnitude increase in abundance from 1992 onwards (*pers. comm.* Ensis Ltd.).

Isoperla grammatica appeared infrequently in UKAWMN samples, and was recorded as an "additional species" by Titmus in May and August 1974, but did not appear in any of the samples collected by the authors (including samples from other microhabitats and from 1987–9). *Isogenus nubecula* was noted only in Gelsthorpe's samples, which lacked the *Diura bicaudata* recorded both in the UKAWMN samples and by the present authors. It is possible that this difference is due to misidentification; Titmus recorded *Diura bicaudata* as an additional species in May and July 1974, but did not record *Isogenus nubecula*.

Baetid mayflies were virtually undetected in any surveys except those of the present authors. No doubt this is due to differences in the timing of samples. *Baetis vernus* completes its larval development over a short period in late spring and summer (Elliott *et al.*, 1988), and may have been present prior to July only as eggs or very small larvae. In the Duddon system, this species occurs in some of the less acid headwaters (Sutcliffe & Carrick, 1973), along with *Leuctra moselyi* (relatively common at Plynlimon) and *Perla bipunctata* (a single specimen was found in the Hafren in May 1991).

The flatworm *Phagocata vitta* was present in the authors' samples from all three streams but was not recorded by Gelsthorpe, Titmus or the UKAWMN. Because this species adheres closely to substratum particles, it is possible that kick-sampling failed to dislodge it, whereas careful hand searching of large particles revealed its presence. There may be a similar explanation for the proportionately greater abundance of Simuliidae in the authors' samples.

The coleopteran *Oreodytes sanmarkii* was recorded in the UKAWMP only from the Hafren (and was not mentioned by Gelsthorpe or Titmus), but was found by the present authors in all three streams. This patchy distribution between studies may be attributable to small differences in the locations of samples: *O. sanmarkii* was found mainly at the edges of streams and in fine sediments (Gee & Smith, 1995) and could have been missed easily in samples taken from the centres of riffles.

Gelsthorpe, Titmus and the UKAWMN recorded *Rhyacophila dorsalis* in the Hafren, but the UKAWMN lacks any record of this species in the Gwy, and Gelsthorpe did not find it in the Hore. In contrast, the present authors encountered it regularly in all three streams (along with *R. septentrionis*) with the greater abundance occurring in October. The former studies did not sample in October and samples taken in spring and early summer may have coincided with the period in which most individuals of this species were pupating or had emerged as adults (Elliott, 1968).

The UKAWMN samples differ from those of Gelsthorpe, Titmus, and the present authors in the greater number of species of caddis recorded. With the exception of the infrequent *Lype* sp. and *Ecclisopteryx guttulata,* all the species in the UKAWMN were recorded in the present authors' survey but did not feature in the samples from coarse substrata in 1985/6 and 1990/1. In the latter study a total of 21 caddis species were collected, but many of these were present mainly in samples taken from stream banks. Over the entire period of this study, between 61 and 72 invertebrate taxa were recorded in each of the streams in either July or October.

Densities of grazer/scraper invertebrates, particularly Ephemeroptera, are often lower when streams or sections of streams are shaded heavily by riparian trees than when they are open and treeless (Newbold *et al.*, 1980; Gurtz & Wallace, 1984; Behmer & Hawkins, 1986; Dudgeon, 1988, 1989, 1994; Bilby & Bisson, 1992). This difference is commonly ascribed to lower algal abundance on shaded stream beds, but in areas of conifer plantation in the British uplands the depletion of some stream invertebrates may be due to low pH or increased concentrations of dissolved aluminium (Harriman & Morrison, 1982; Stoner *et al.*, 1984). Against this background it is not surprising that Gelsthorpe and Titmus found few Ephemeroptera within the Hafren forest (although many further downstream), and that the present authors found a large difference in density of *Baetis vernus* between the moorland Gwy and the forested Hore and Hafren in 1985/6.

Removal of trees from a large part the catchment of the Hore might have been expected to result in a change of composition of the stream invertebrate assemblage, so that it converged in character with that of the moorland Gwy and diverged from the Hafren. Such a change might have followed an increase in the abundance of algae, an increase in pH, a decrease in dissolved aluminium, or even an increase in stream temperature (which is generally higher in summer in open streams). In practice, clear felling in the Hore led to a slight reduction in pH (accompanying a marked increase in nitrate) and an increase in dissolved aluminium (Neal *et al.*, 1992a), along with the anticipated increase in stream temperature (Neal *et al.*, 1992b). The epilithic algal biomass was higher in the moorland Gwy than in the clear-felled Hore or the undisturbed, forested Hafren (data are not available for the pre-felling period), but there was no significant difference between biomasses in the Hore and the Hafren (Anne L. Davies, *pers. comm.*). However, the proportion of filamentous green algae in the epilithon was higher in the Gwy and the Hore than in the Hafren. Alongside these patterns in environmental conditions, there was little change in the composition of the invertebrate community in the Hore. Although there was an increase in abundance in *Baetis vernus* in the Hore after the felling, a similar increase occurred in the undisturbed Hafren, so it cannot be interpreted as a direct consequence of felling. It is intriguing that the sampling station on the Hafren that yielded over 70% of the individuals of *Baetis vernus* during the entire duration of the authors' survey is also the site at which a small population of trout was found unexpectedly (SN838884: Crisp & Beaumont, 1996).

A general conclusion is that afforestation of streams in the Plynlimon area is associated with differences in invertebrate assemblages, and that some of these differences are consistent with previous comparisons of forested and unforested streams. There was no evidence of lower diversity in the forested streams, at least in terms of taxon richness. Manipulation of the environment by extensive felling in the Hore catchment does not appear to have changed the composition of the invertebrate assemblage. In this regard the evidence does not support the 'templet' type of conceptual framework which is sometimes used to link organisms and their environment (Wootton & Gee, in press). This apparent failure of the data to match expectations mirrors a lack of response of invertebrates to manipulation of stream water chemistry (Rundle *et al.*, 1995) and could be due to several causes. The expectations may be based on correlative evidence which is not underpinned by causative links. Alternatively, it is possible that the speed or extent of the response of invertebrate populations to changes in the stream environment is constrained by the dynamics of movements of propagules (adult female insects bearing eggs) between streams. This last possibility could be interpreted as a failure to match the scale of the study to the scale of the processes that drive community change in these headwater streams, but very little is known of the dispersal of adult insects within and between catchments.

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