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The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye in relation to environmental factors

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SUMMARY. 1. Macroinvertebrates were sampled from three habitats at forty-five sites in the catchment of the Welsh River Wye. Species assemblages were ordinated by DECORANA, classified by TWINSPAN and related to physico-chemical factors using correlation and multiple discriminant analysis respectively.

2. DECORANA axis 1 was correlated with pH or total hardness, whilst axis 2 correlated with slope or distance from source. TWINSPAN groupings were also related to hardness and, to a lesser extent, slope. Assemblages at soft-water sites (<15 g m^{-3} $CaCO_3$) were composed mostly of Plecoptera but at hard-water sites, even at high slope (>10 m km^{-1}), the fauna was dominated numerically by Ephemeroptera, net-spinning Trichoptera, Mollusca and Crustacea.

3. We suggest that our data do not support the River Continuum Concept unless there are modifications to allow for multiple gradients.

Introduction

Attempts have been made recently to establish predictive relationships between the macroinvertebrate faunas and physico-chemistry of running waters (Furse *et al.*, 1984; Wright *et al.*, 1984). Potential benefits include the ready assessment of biological resources for conservation purposes from physico-chemical data, and the detection of pollution through differences between predicted and actual faunal assemblages.

Although such predictive models have been sought at a national (Wright *et al.*, 1984), European (Personne, 1979) and holarctic level (Cushing *et al.*, 1980), they might also be desirable for important river catchments. The River Wye, for example, is of considerable value as a water resource, and for nature conservation and freshwater fisheries (Edwards & Brooker, 1982). However, there have been no attempts to derive models which could be used to assess biological changes in the Wye's catchment such as those which result from impoundment, land-use change, surface-water acidification or other influences (Brooker & Morris, 1980; Inverarity, Rosehill & Brooker, 1983; Stoner, Gee & Wade, 1984; Ormerod & Edwards, 1985).

Additionally, there has recently been much research into the organization and structure of macroinvertebrate assemblages in running waters, particularly in relation to the relative influences of abiotic and biotic factors (e.g. Vannote *et al.*, 1980; Winterbourn, Rounick &

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Cowie, 1981; Culp & Davies, 1982; Hawkins, Murphy & Anderson, 1982; Townsend, Hildrew & Francis, 1983; Hildrew *et al.*, 1984; Bronmark *et al.*, 1984; Marchant *et al.*, 1985; Minshall *et al.*, 1985; Statzner & Higher, 1985, 1986). However, only a few of these studies have been conducted in the U.K. (Townsend *et al.*, 1983; Hildrew *et al.*, 1984; Wright *et al.*, 1984).

This paper describes assemblages of macroinvertebrates in the catchment of the River Wye in 1982 and relates them to environmental factors. The analytical procedures follow those recommended by Green & Vascotto (1978) and developed by Wright *et al.* (1984) and Furse *et al.* (1984).

The study area

All studies were undertaken in or adjacent to the catchment of the River Wye, the general area of which has been described elsewhere (Edwards & Brooker, 1982; Ormerod, 1985). The river rises on Plynlimon, in Powys, at 677 m O.D. and flows south east for 250 km to join the Seven estuary at Chepstow, Gwent. In addition to the impounded River Elan, there are four principal tributary systems and four distinct areas of high relief and high altitude (300–800 m O.D., Fig. 1). The predominantly rural catchment of 4183 km^2 has a diverse geological structure (Fig. 2), three areas of which are important to this study: the Ordovician and lower Silurian shales and mudstones (Llandovery series), the relatively calcareous Wenlock beds, and the Devonian and calcareous Old Red Sandstone (ORS). Water quality in the tributaries draining these areas differs between mineral poor (total hardness 8–25 g $CaCO_3$ m^{-3}), intermediate (25–90 g $CaCO_3$ m^{-3}) and mineral rich (90–220 g $CaCO_3$ m^{-3}).

Land-use in the catchment is dominated by temporary or permanent grassland and rough grazing, although conifer forests have been

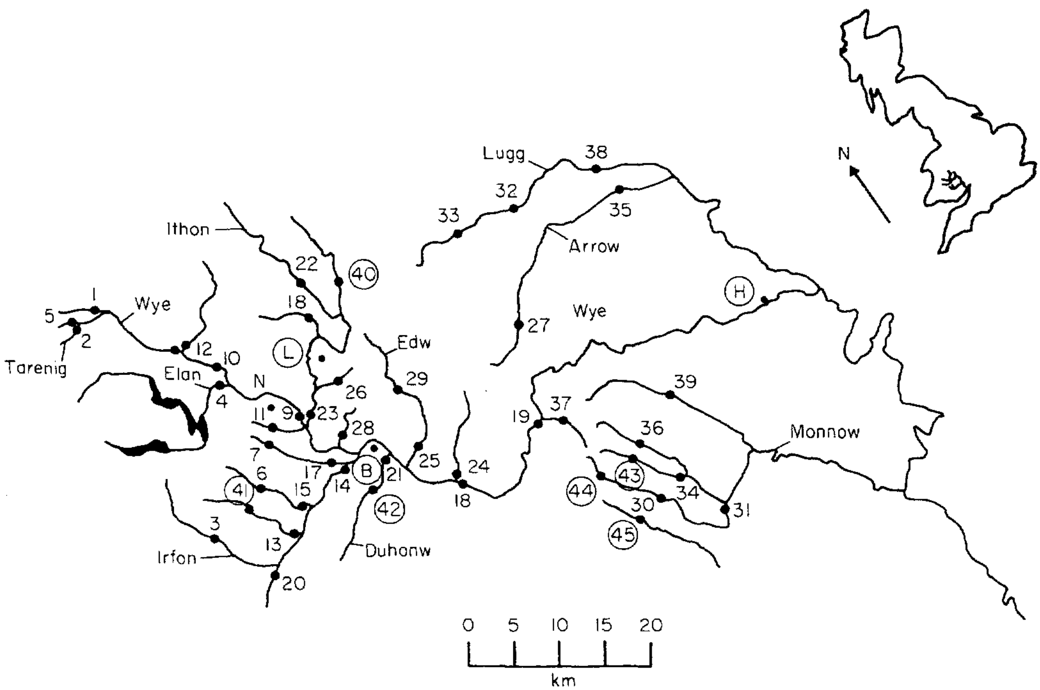

FIG. 1. The study area and sampling locations. Sites 1–39 had water quality data available and are numbered in increasing order of conductivity. Sites 40–45 had water quality data available within 5 km. Sites 7, 9, 11, 14, 17, 23, 28 and 42 were used for temperature studies. H=Hereford, B=Builth Wells, L=Llandrindod Wells, N=Newbridge-on-Wye (air temperature site).

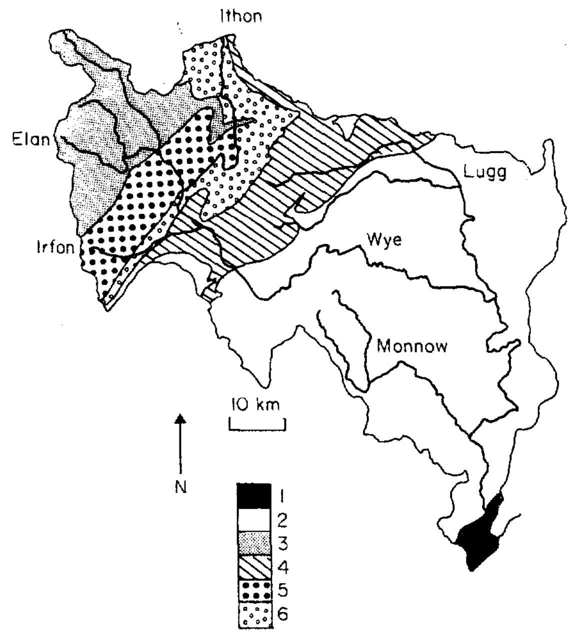

FIG. 2. Principal solid geology of the catchment of the River Wye. 1, Triassic and Carboniferous; 2, Old Red Sandstone; 3, Silurian (Ashgill and Caradoc); 4, Silurian (Ludlow); 5, Ordovician (Llandovery); 6, Silurian (Wenlock).

planted since the 1940s and now cover 25–50% of the drainage areas of some of the Wye's tributaries. The consequence for water quality have been discussed elsewhere (Ormerod & Edwards, 1985).

The Grwyne Fawr, added to the study areas as a hard-water stream draining on afforested catchment (a type unavailable in the Wye system), flows into the River Usk and, in its upper reaches, runs parallel and directly adjacent to the Monnow sub-catchment of the Wye (site 45, Fig. 1).

Methods

Forty-five sites were selected on the basis of altitude, stream size, underlying geology and land-use, where possible minimizing correlations between these factors. For example, high altitude sites on small streams were included both on base-rich and on base-poor rocks, and draining both from moorland and from coniferous forest. The influence of each factor on the data-set could then be assessed independently.

Environmental factors

For each site, distance from source, altitude and slope (over 4–6 km) were derived from 1:50,000 Ordnance Survey Maps. Discharge categories (average dry weather flow: ADF) were determined from maps produced during the River Pollution Survey of England and Wales (H.M.S.O., 1978) and stream link magnitudes (Shreve, 1968) were calculated by summing all the first order streams (shown on 1:50,000 maps) which contributed to the flow at any site.

The proportions of the river-bed at each site composed of bedrock, boulders (>500 mm particle diameter), cobbles (100–500 mm), pebbles (10–100 mm) and sand or gravel (1–10 mm) were estimated by eye during the spring sampling run (see below). Depths were measured at each site in representative riffles and flats on both sampling occasions (i.e. two values per visit), and means were calculated from the four resulting values (see Ormerod, 1985).

Chemical data were provided by the Welsh Water Authority, samples being taken at all sites on more than six, and usually more than fifteen to twenty occasions throughout the year. At twenty-two sites values were available from contemporaneous sampling programmes; at a further seventeen sites no data were available after 1979. At the remaining six sites (nos. 40–45, Fig. 1), although contemporaneous data were available, the biological and chemical sites were separated by up to 5 km.

It was impracticable to monitor stream temperatures at all the sites. However, eight (Fig. 1) which gave a range of stream size, altitude and water chemistry were visited at weekly intervals between 11 January and 20 December 1982 and temperatures were read from maximum–minimum thermometers. Air temperatures were monitored over the same period at Newbridge-on-Wye (198 m O.D., SO 009 586) using a maximum–minimum thermometer housed in a white Stevenson screen.

Macroinvertebrates

Each site was visited for macroinvertebrate sampling in spring (25 February to 29 March) and autumn (13–29 October), 1982. Following other classificatory studies in the U.K. (Wright *et al.*, 1984), the principal objective of the sampling strategy was to obtain a comprehensive species list for each site within the limitations of time required for sorting and identification. Because some taxa are associated with parts of the river channel other than riffles (Jenkins & Wade, 1981; Jenkins, Wade & Pugh, 1984; Logan & Brooker, 1985; Ormerod, 1985), collections were made from riffles, river margins and flats (slow runs) at each site, one 3-min kick/sweep sample being taken from each habitat using a hand-net (mesh 440 μm, frame size 450×350 mm). All samples were fixed immediately in 4% formalin.

In the laboratory, coarse organic debris was removed by flotation and sieving and the following groups were identified to species: Tricladida, Mollusca, Hirudinea, Malacostraca, Ephemeroptera, Plecoptera, Coleoptera, Trichoptera and Megaloptera.

Statistical analysis

Environmental factors. Prior to any further analysis, the statistical distribution of each variable was examined graphically and transformations were applied which gave the best approximation to normality (Table 1). Correlations between variables were identified using Principal Components Analysis (Kim, 1975; SPSS Inc., 1984; see Ormerod, 1985) and, where appropriate, the following key variables were selected to minimize redundancy and were used to examine the relationships between stream physico-chemistry and macroinvertebrate assemblages: log of slope; log of altitude; substratum category; log of total hardness; square root of phosphorus concentration.

Differences in temperature regimes between sites were assessed by regressing mean weekly river temperature on mean weekly air temperature. Comparisons between sites or site-groups were then made by *t*-tests between the

TABLE 1. Transformations applied and the abbreviations for each variable name

Variable	Transformation	Abbreviated name
Mean conductivity	Log	LGCN
Mean total hardness	Log	LGHD
Mean pH	None	pH
Minimum pH	None	MINPH
Mean nitrate	Log	LGNT
Mean orthophosphate	Square root	RTPS
Stream link	Log	LGSLK
Slope	Log	LGSLP
Mean depth	Log	LGDEP
Distance from source	Log	LGDFS
Altitude	Log	LGALT
Substratum category	None	SUB
Discharge category	None	DIS

slopes and intercepts of the regression equations (Sokal & Rohlf, 1981; see Ormerod, 1985).

Macroinvertebrates. Species occurrences at each site were listed by combining habitat and seasonal data. The combined data were then ordinated by DECORANA (Hill, 1979a) and classified by TWINSPAN (Hill, 1979b) using presence/absence at specific or generic level. Where any doubt existed over specific identification (e.g. *Ecdyonurus dispar/venosus*), generic identifications were used for all occurrences of the taxon in question. Classification by TWINSPAN arranges site-groups into a hierarchy on the basis of their taxonomic composition, and species are classified simultaneously on the basis of their occurrence in site groups. Indicator species are also identified, these showing the greatest difference between site-groups in their frequency of occurrence.

In ordination by DECORANA, sites are arranged into an objective order, those with similar taxonomic composition occurring most closely together. An axis score is produced which can be used in relating the ordination to environmental factors. In this study, DECORANA was used only after invoking a 'down weighting' option which minimized the influence of rare species (Hill, 1979a). Further details of TWINSPAN and DECORANA, and their advantages over similar techniques are given by Wright *et al.* (1984) and Furse *et al.* (1984).

The relative strengths of DECORANA axes were given by eigenvalues and the relative importance of each axis, in explaining variance in the entire data-set, was derived by dividing its eigenvalue into the total eigenvalue for all the axes combined. The positions of sites along axes, and their overall lengths, were given in standard deviations. DECORANA axes were related to environmental variables using the product-moment correlation coefficient (Sokal & Rohlf, 1981).

The TWINSPAN procedure, which included the simultaneous classification of sites- and species-groups, was arrested at level 3 beyond which groupings ceased to be ecologically meaningful. Relationships between the TWINSPAN site-groupings and the five key environmental variables were investigated by Multiple Discriminant Analysis (MDA) using the SPSS^X routine 'DISCRIMINANT' (SPSS Inc., 1983). The procedure identifies linear combinations of variables which discriminate most strongly between site groups defined *a priori* on the basis of classification; contributions by individual variables to the discrimination are judged according to weighting coefficients. Only those discriminant functions which were significant at $P<0.1$, when tested against Wilk's lambda (Klecka, 1975), were used in the analysis. The prediction of TWINSPAN site-group membership was concomitantly investigated using the discriminant functions derived from environmental data alone. Preliminary MDA indicated that pH or LGCON (log conductivity) could have been substituted for LGHD (log total hardness), and LGDFS (log distance from source) or LGSLK (log stream link magnitude) substituted for LGSLP (log slope), to give results which were comparable, although marginally less successful, in predicting TWINSPAN group membership.

Results

Ordination

The primary and secondary axes of ordination, which together explained 72% of the variance in the data-set, were respectively 1.91 and 1.22 standard deviations in length and represented changes in taxonomic composition of approximately 75% and 55% (Table 2). The

TABLE 2. Eigen-values, cumulative percentage variance explained and lengths (standard deviations) of each DECORANA axis

	Eigenvalue	Cumulative % variance explained	Length (SD)
Axis 1	0.125	42.5	1.91
Axis 2	0.084	71.1	1.22
Axis 3	0.053	89.1	1.38
Axis 4	0.032	100.0	0.92

TABLE 3. Product–moment correlation coefficients between site scores on DECORANA axes 1 and 2 and environmental variables

Variable	Axis 1	Axis 2
LGSLP	0.119	−0.787***
LGALT	0.508***	−0.463**
LGSLK	−0.031	0.643***
DIS	0.007	0.718***
SUB	0.245	0.229
LGDEP	−0.243	0.703***
LGDFS	−0.156	0.738***
LGCN	−0.907***	−0.071
LGHD	−0.915***	−0.098
pH	−0.885***	−0.094
MINPH	−0.885***	−0.037
LGNIT	−0.784***	0.123
RTPS	−0.135	0.226

** $P<0.01$; *** $P<0.001$.

remaining axes (3 and 4) together explained <30% of the variance and could not be related clearly to any of the measured environmental factors. By contrast, axis 1 correlated strongly with the total hardness/pH group of variables (e.g. axis 1: log hardness $r=-0.915$, $P<0.001$) whilst axis 2 correlated strongly with the slope and stream link group of variables (e.g. axis 2: log slope, $r=0.787$, $P<0.001$) (Table 3); both axes correlated significantly, although less strongly, with altitude. Axis 1 could therefore be interpreted as detecting changes in macroinvertebrate assemblages in relation to spatial changes in total hardness and pH whilst axis 2 detected changes in relation to slope and stream link magnitude. When these axes were plotted together (Fig. 3), some grouping of sites was apparent which corresponded with the TWINSPAN classification.

Classification

Six site-groups were produced at TWINSPAN level 3 and comparison with the DECORANA axes indicated that the classification was strongly related to water hardness–pH and, to a lesser extent, to site slope and stream link magnitude (Figs. 4 and 5; Tables 3 and 4). Sites in groups A and B had soft waters (<12.5 g $CaCO_3$ m^{-3}) and moderate to high slopes (4.7–19.0 m km^{-1}) and were situated on the uppermost reaches of the River Wye and its tributaries (Bidno, Tarenig) and on the upper River Irfon and River Elan. Group C was composed of sites with slightly harder waters (20–50 g $CaCO_3$ m^{-3}) than A or B and were situated on the Irfon sub-catchment, on the River Marteg, the River Clwedog (Ithon sub-catchment) and on the Wye at Rhayader and Newbridge. Group D sites had low slopes

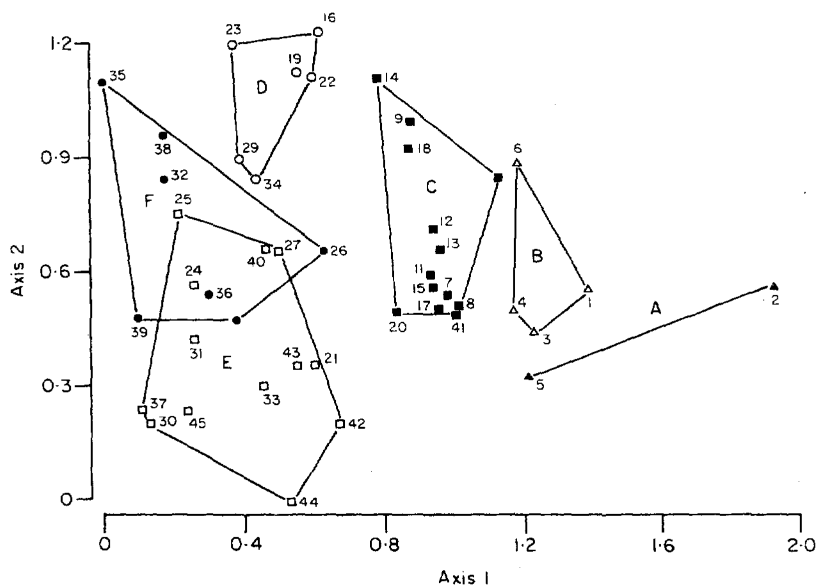

FIG. 3. DECORANA axis 2 plotted against axis 1 for forty-five sites in the Wye catchment, numbered according to Fig. 1. The symbols, letters, and polygons correspond to level 3 TWINSPAN groups (Fig. 4). See Table 3 for interpretation of axes.

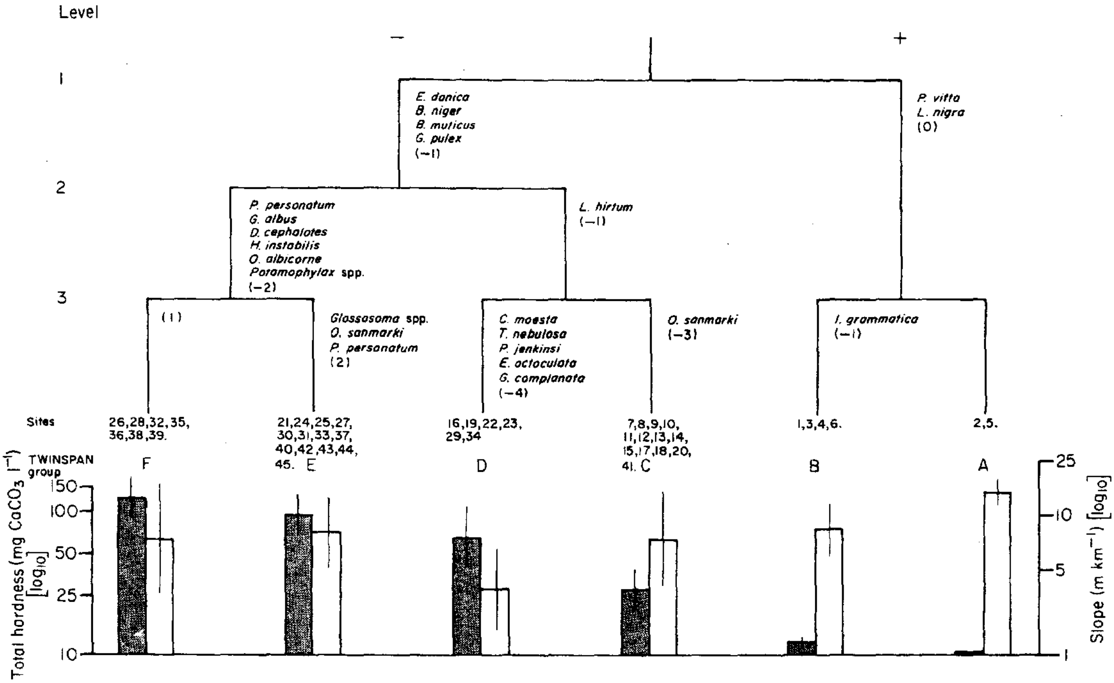

FIG. 4. Classification of forty-five sites in the Wye catchment as revealed by TWINSPAN to level 3. The indicator species are shown at each level and the values in parentheses give the scores required for classification at each dichotomy. The histogram shows mean values (±1 SD) for total hardness (shaded) and slope (unshaded) of the sites in each group.

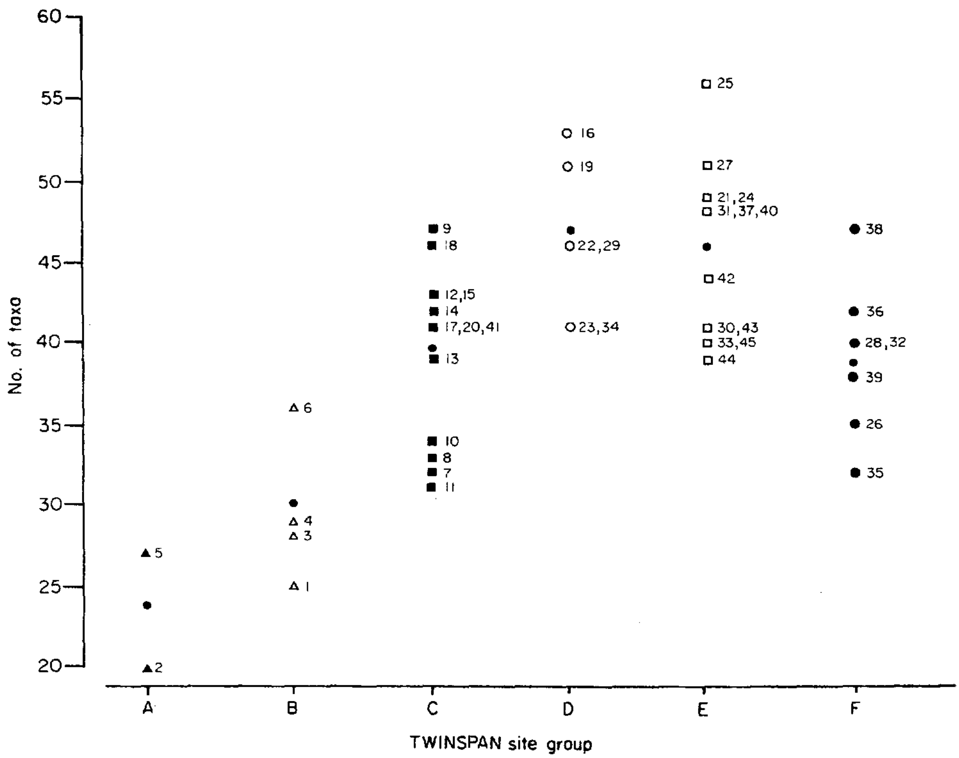

FIG. 5. The number of taxa recorded at each site, arranged by TWINSPAN site-group. The means for each group are indicated by unnumbered points.

TABLE 4. Mean values of thirteen environmental variables for each TWINSPAN at group at level 3. Asterisked values are back transformed.

	Twinspan site group					
Variable	A	B	C	D	E	F
*LGSLP (m km^{-1})	13.1	9.6	6.6	2.9	12.2	6.4
*LGALT (m O.D.)	320	235	174	148	176	136
*LGSLIK	15	57	27	125	22	18
DIS cat.	2	4	3	5	2	3
SUB cat.	3.5	3.5	3.5	3.5	3.5	3.5
*LGDEP (cm)	21	19	24	39	21	28
*LGDFS (km)	7.5	17.5	15.1	35.0	11.4	13.7
*LGCN (μS cm^{-1})	47.9	47.3	84.1	174.8	224.6	303.5
*LGHD (g $CaCO_3$ m^{-3})	10.5	12.5	27.8	69.9	102.3	132.2
pH	6.4	6.5	7.1	7.6	7.7	7.8
MINPH	5.0	5.5	6.2	6.8	7.1	7.2
*LGNIT (g m^{-3})	0.22	0.32	0.51	0.93	1.25	2.27
*RTPS (g m^{-3})	0.09	0.14	0.09	0.19	0.11	0.21

(<5 m km^{-1}) and moderate to high hardness (37–150 g $CaCO_3$ m^{-3}) and were on the lower Wye, the River Ithon, the upper River Edw and River Monnow. Group E consisted of sites with moderate to high slopes (6–37.2 m km^{-1}) and high hardness (59–170 g $CaCO_3$ m^{-3}) on the River Edw, River Aran, Bach Howey, upper River Lugg and on tributaries draining from the ORS Black Mountains plateau. Group F was also composed of hard-water sites (76–220 g $CaCO_3$ m^{-3}) on the lower Rivers Arrow and Lugg and on tributaries in other sub-catchments (Howey Brook, Builth Road Dulas, Escle, Dore).

There was no evidence that the classification patterns reflected temperature. Although two distinct thermal regions could be recognized for small and large streams (Table 5), sites characterized by similar temperatures but different chemistry occurred in different TWINSPAN groups (e.g. sites 7, 11, 28, 42 in groups C, F, E; sites 14, 17 in groups C, D). Similarly sites with different temperature regimes (e.g. 14, 17), but similar water chemistry, occurred in the same TWINSPAN groups (Table 5; Fig. 4).

The number of taxa recorded at sites in each TWINSPAN group generally increased between groups A and E and decreased slightly in group F (Fig. 5). Only the most widely occurring taxa were present in groups A and B (Fig. 6), although *Leuctra nigra* (Olivier) and *Phagocata vitta* (Duges) were indicator species for these site-groups and *Chloroperla tripunctata* (Scopoli) was more frequent in A, B and C than in D, E and F. Several ephemeropteran taxa, including the negative indicators at TWINSPAN level 1 (*Baetis niger* (L.), *B. muticus* (L.) and *Ephemera danica* Müller), were confined to groups of C–F, along with the trichopterans *Hydropsyche instabilis* (Curtis) and *Drusus annulatus* (Stephens), and several molluscs (*Potamopyrgus jenkinsi* (Smith), *Lymnaea peregra* (Müller), *Pisidium subtruncatum* Malm and *Gyraulus albus* (Müller)). *Gammarus pulex* (L.) was also most frequent at sites in groups C–F and absent from sites in group A (Figs. 4 and 7).

TABLE 5. Generalized regression ($y=a+bx$) of weekly mean river temperature on air temperature at Newbridge-on-Wye for (A) sites with high gradient/low stream link. (B) Sites with low gradient/high stream link. Equations from sites within each group had slopes and intercepts which did not differ significantly and they were combined.

Combined sites	$a\pm95\%$ C.I.	$b\pm95\%$ C.I.	n	100 r^2
(A) 7, 11, 28, 42	3.40±0.40	0.715±0.039	159	89.1
(B) 14, 23	3.07±0.77	0.942±0.075	77	89.3
Comparison (t-statistic)	0.633^{NS}	−5.33***		

*Variances unequal (F ratio=1.78**).

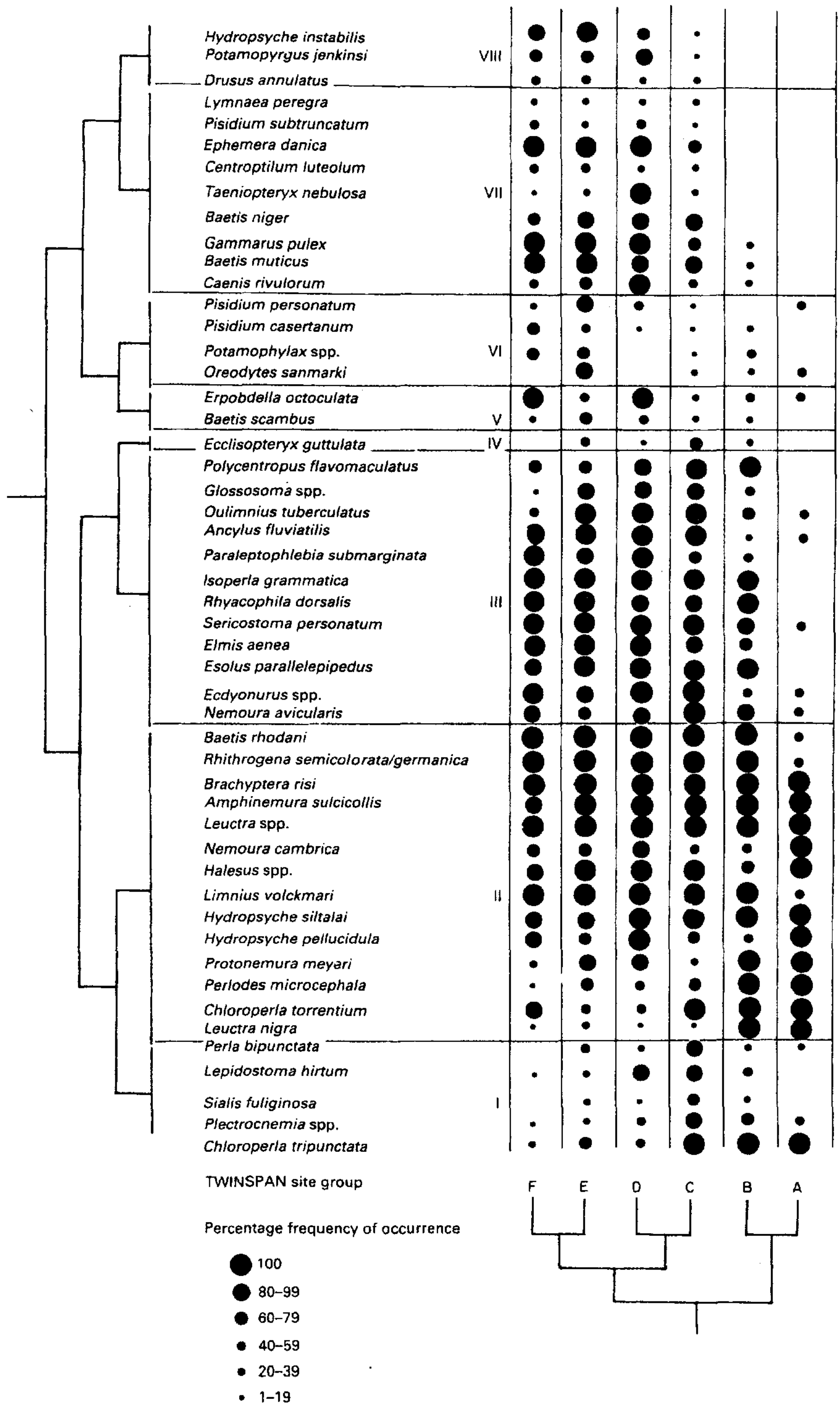

FIG. 6. Classification of species and site groups by TWINSPAN. The circles show the percentage frequency of occurrence of each taxa between the sites in each group (only the fifty most widely occurring taxa are shown).

An examination of the proportional representation of taxa and individuals confirmed that groups A and B were dominated by plecopterans, whilst ephemeropterans, molluscs and crustaceans (mostly *Gammarus pulex*) became increasingly common and abundant in groups B–F (Table 6).

Multiple discriminant analysis

MDA was successful in predicting between 100% (level 1) and 69% (level 3) of the forty-five sites to the correct TWINSPAN site-group using five environmental variables and one discriminant function extracted at

TABLE 6. Proportional representation of taxa and individuals for each TWINSPAN site-group (mean percentage per site ±SD after arcsine transformation and back transformed)

(a) Taxa

TWINSPAN group	A	B	C	D	E	F
Taxonomic group						
Tricladida	4.3	4.1	1.1	0.0	0.9	1.7
	(0.9)	(2.9)	(1.3)	(0.0)	(1.3)	(1.7)
Hirudinea	2.5	1.5	1.3	6.3	1.7	4.5
	(3.5)	(1.8)	(2.3)	(3.8)	(1.9)	(2.3)
Mollusca	3.9	1.5	4.3	8.4	8.9	11.4
	(5.2)	(1.8)	(2.1)	(2.1)	(3.0)	(6.2)
Crustacea	2.5	1.7	1.9	2.8	4.0	4.4
	(3.5)	(2.0)	(1.1)	(0.8)	(1.0)	(1.4)
Ephemeroptera	11.1	13.4	20.9	24.0	24.1	21.9
	(15.7)	(3.3)	(3.2)	(1.8)	(3.5)	(1.2)
Plecoptera	39.2	35.0	26.8	20.4	22.4	20.9
	(8.2)	(3.6)	(2.4)	(2.8)	(4.0)	(6.6)
Coleoptera	16.7	13.7	13.5	9.7	12.3	9.1
	(2.4)	(5.1)	(2.2)	(1.4)	(1.9)	(1.4)
Trichoptera	19.9	28.7	29.7	28.1	26.2	26.1
	(7.2)	(3.1)	(3.9)	(3.9)	(4.9)	(5.9)

(b) Individuals

TWINSPAN group	A	B	C	D	E	F
Taxonomic group						
Tricladida	1.4	0.9	0.0	0.0	0.7	0.1
	(0.1)	(0.3)	(0.0)	(0.0)	(0.7)	(0.1)
Hirudinea	0.1	0.1	0.1	2.1	0.1	0.5
	(0.1)	(0.1)	(0.2)	(2.3)	(0.1)	(0.9)
Mollusca	0.6	0.1	0.4	4.8	1.2	10.4
	(0.8)	(0.1)	(0.3)	(7.2)	(0.8)	(10.1)
Crustacea	0.2	0.2	1.6	6.9	14.6	34.8
	(0.3)	(0.3)	(3.7)	(5.4)	(19.6)	(23.3)
Ephemeroptera	2.0	14.7	46.0	48.9	46.4	35.6
	(2.9)	(19.4)	(14.5)	(16.7)	(12.1)	(14.2)
Plecoptera	87.8	69.7	24.3	9.1	18.4	10.6
	(6.4)	(2.4)	(10.9)	(7.0)	(10.1)	(14.5)
Coleoptera	4.3	3.5	9.8	7.3	4.2	1.9
	(4.6)	(3.5)	(3.4)	(3.4)	(2.3)	(0.7)
Trichoptera	3.2	10.6	17.3	20.6	14.5	5.7
	(1.1)	(4.7)	(16.5)	(11.7)	(9.2)	(4.2)

TABLE 7. The percentage of sites predicted to the correct TWINSPAN group using MDA with five environmental variables. The number of significant discriminant functions is shown for $P \leq 0.05$ except where stated.

Level of division	No. of TWINSPAN groups	No. of significant discriminant functions	Sites correctly predicted
1	2	1	100
2	3	1	93.3
3	6	1	68.9
3 ($P \leq 0.10$)	6	2	86.7

TABLE 8. Standardized discriminant function coefficients for environmental variables at each TWINSPAN level of division. The functions were significant at $P \leq 0.05$ except where stated.

	Function 1			Function 2
Variable	Level 1	Level 2	Level 3	Level 3 ($P \leq 0.10$)
LGSLP	−0.043	0.672	0.217	0.956
LGALT	−0.407	−0.542	−0.445	−0.148
SUB	0.066	−0.062	0.036	−0.184
LGHD	0.884	0.990	0.973	0.058
RTPS	0.010	−0.037	0.261	0.465
% variance explained	100	95.5	90.2	82.8
Canonical correlation	0.719	0.904	0.943	0.651

$P<0.05$ (Table 7). Total hardness was a prominent component, on the basis of the standardized discriminant function coefficients, of the first discriminant function at all levels of division (Table 8). A further discriminant function for TWINSPAN level 3 was extracted at $P<0.1$ and was related to slope (Table 8).

Discussion

The results and analysis presented here describe clear relationships between macroinvertebrate assemblages and environmental factors, both by correlation between site ordination and environmental gradients, and by a multiple discriminant analysis which showed relationships between a biological classification system and discriminant functions derived solely from physico-chemical factors. The latter analysis supports Wright *et al.* (1984) in that macroinvertebrate assemblages in running waters can be accurately predicted from environmental data alone for the purposes of detecting pollution (Hawkes, 1975), assessing resources (Ratcliffe, 1977) and managing the aquatic component of river corridors (Brooker, 1982). There has been no attempt at such predictions in a single river-system.

Of the physico-chemical variables which were recorded, substratum category showed no correlation with the DECORANA axes and was not prominent in influencing TWINSPAN classification, according to MDA. This contrasts with the findings of Wright *et al.* (1984) who recorded a significant correlation between substratum characteristics and the ordination of 268 sites on running waters throughout the U.K. and with other authors who have also noted the importance of the substratum in influencing the abundance and diversity of benthic macroinvertebrates (Milner *et al.*, 1981). The confinement of the present study to one catchment, the location of all the study sites on fast-flowing rivers, and the incorporation of several habitat types at each site in the sampling regime, combined to reduce the between-site variability of substratum types included.

Whilst river temperature has been recorded elsewhere as an important influence on the distribution of some macroinvertebrate species (e.g. Hildrew & Edington, 1979), the incomplete survey of temperature during the present study precluded a full consideration of its influence on the ordination and classification patterns. However, there was evidence that temperature did not exert a strong influence, over the range considered, on site classification (Table 5).

Brooker & Morris (1980) noted a positive relationship between the concentration of total dissolved solids and the abundance and diversity of macroinvertebrates in the River Wye but were unable to separate the effects of concomitant downstream changes such as altitude, stream link magnitude, habitat diversity and slope. In the present study such physical variables were less prominent than water chemistry in correlations with macroinvertebrate assemblages. Additionally, hard-water sites at altitudes over 250 m O.D. on the Black Mountains plateau (part of TWINSPAN group E), for example, were separated in TWINSPAN and DECORANA from physiographically similar sites with soft-waters in the northern part of the catchment (TWINSPAN groups A and B). This finding supports earlier observations that the geology underlying the Wye catchment, with its effect on water chemistry, is of considerable importance to patterns of macroinvertebrate distribution in the main river (Brooker & Morris, 1980; Edwards & Brooker, 1982).

The results also support the conclusions of other authors (Sutcliffe & Carrick, 1973; Ziemann, 1975; Townsend *et al.*, 1983) that water chemistry, particularly variables associated with pH and water hardness, correlate strongly with the distribution of some macroinvertebrate taxa and species assemblages. Most notable was the scarcity of *Gammarus pulex* and several species of mollusc, ephemeropteran and net-spinning caddis in acidic-soft waters. Whilst simple bivariate relationships between macroinvertebrate distribution patterns and chemical variables were confounded by interrelationships amongst several determinands (pH, hardness, conductivity, nitrate-nitrogen), it is noteworthy that the six sites isolated at the primary TWINSPAN division were characterized by 'fluctuating pH' (Sutcliffe & Carrick, 1973) and also by the most impoverished macroinvertebrate faunas (Table 4, Fig. 5). Moreover, these sites also lie within an area of Wales which has been identified as being 'at risk' from surface-water acidification (Stoner *et al.*, 1984) and three are influenced by drainage from coniferous forests which may have led to an increase in acidity over recent decades with possible consequences for their macroinvertebrate faunas (Stoner *et al.*, 1984; Ormerod & Edwards, 1985). It is of interest that one hard-water stream draining a catchment dominated by coniferous forest (Grwyne Fawr, site 45) supported a diverse fauna and occurred in TWINSPAN group E. Further studies of the relationships between acidity, hardness and macroinvertebrate distributions are now in progress in soft-water streams in or adjacent to the Wye catchment.

It is not possible, on the basis of these results, to determine the nature of any causal relationships between macroinvertebrate distributions and pH or total hardness. Effects involving physiology or food supplies have been proposed in other studies. Sutcliffe (1978) noted that osmoregulatory stress could exclude gammarids from soft, acidic waters and there could be similar effects on Ephemeroptera. The latter are known to have chloride cells with an osmoregulatory function (Komnick, Rees & Abel, 1972) and Fiance (1978) thought that osmoregulatory stress was implicated in the low abundance and reduced growth of *Ephererella funeralis* McDunnough in an experimentally acidified stream (Hall *et al.*, 1980). In the latter study, a reduction in the density of benthic macroinvertebrates accompanied an increase in algal standing-crop and occurred prior to a reduction on hyphomycete density, indicating that the effect of acidification did not operate through the food supply and hence could have been physiological (Hall *et al.*, 1980). Similarly, Ormerod *et al.* (1987) recently demonstrated that elevated aluminium concentrations and low pH had a short-term influence (24 h) on the drift and mortality of some invertebrates, notably ephemeropterans, in a soft-water stream adjacent to the Wye. Nevertheless, there is still evidence for trophic effects: the slow breakdown of cellulose at low pH, noted in other rivers (Egglishaw, 1968; Hildrew *et al.*, 1984) has recently been described in the upper Wye (Stanyer, 1983). Moreover, observations by other authors (Sutcliffe & Carrick, 1973; Townsend *et al.*, 1983), that those insects which are scarce in soft, acidic waters are frequently herbivores or filter-feeders, is not refuted by the present study.

It might have been anticipated from the 'River Continuum' concept (Vannote *et al.*, 1980) that stream link magnitude or slope would have been a dominant correlate with the ordination and classification patterns produced in this and other studies (Wright *et al.*, 1984; Furse *et al.*, 1984). Instead, stream link magnitude emerged as a factor secondary in importance to pH and hardnesss (this study) or alkalinity (Wright *et al.*, 1984). These results infer that differences between rivers, or between tributaries within a catchment, can be at least as pronounced as differences along rivers. Whilst predictions based on the continuum concept are prevented by the limited downstream extent of sites in this study, and of British rivers as a whole, proponents of the concept should accept that 'river continua' can have markedly different origins according to catchment characteristics and water chemistry. Similar amendments to the continuum concept have been proposed elsewhere (Culp & Davies, 1982; Magdych, 1984) and its proponents recently accepted the need for a modification which allowed for multiple gradients (Minshall *et al.*, 1985).

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