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The effects of water abstractions on invertebrate communities in U.K. streams

E. Castella[1], M. Bickerton[2], P. D. Armitage[3] & G. E. Petts[4]
[1] *Laboratoire d'écologie et de biologie aquatiques, Université de Genève, 18 chemin des Clochettes, CH-1206 Genève, Switzerland*
[2] *Freshwater environments research group, Department of Geography, University of Technology, Loughborough, Leicestershire, LE11 3TU, UK*
[3] *Institute of Freshwater Ecology, River Laboratory, East Stoke, Wareham, Dorset, UK*
[4] *School of Geography, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK*

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Abstract

There are increasing concerns about the ecological effects of water abstraction and in the UK, these concerns have been hightened by the 1976, 1984 and 1988–92 droughts. This paper assesses macroinvertebrate and environmental changes induced by surface and groundwater abstractions on 22 streams throughout the UK.

The approach involved comparative research to assess differences between reference and impacted sites.

Using a database comprising 204 sets of biological and environmental data (89 taxa and 16 environmental variables) a preliminary ordination using principle components analysis clearly differentiated three types of sites: upland, lowland and an intermediate type. At this scale, any effects of abstractions on invertebrate communities are shown to be insignificant relative to regional controls. A simultaneous ordination of the environmental and faunal differences between pairs of sites was undertaken separately for each of the three regional groups. Differences are considered as vectors having both direction and amplitude and the analysis elucidates common patterns in the faunal and environmental data. Important changes were observed in two situations: upland streams affected by major diversions as part of hydro-power schemes in Scotland and lowland rivers impacted by groundwater abstractions.

No strong patterns of change (either in amplitude or orientation) were demonstrated within any of the taxonomic groups. However, within the upland type some rheophilous taxa were shown typically to be reduced in abundance at impacted sites. Within the lowland type, a consistent pattern in the dataset is demonstrated by a group of taxa that are reduced in abundance at the impacted sites.

Introduction

Increasing abstractions of water directly from rivers and streams, and indirectly from groundwater and surface reservoirs, have generated concern for the conservation of lotic and riparian biota. Particular concerns have been raised about the effects of out-of-basin transfers, groundwater pumping, and consumptive abstractions for irrigation. Aquatic macroinvertebrates play a crucial role in the energy dynamics of lotic systems, acting as shredders, collectors and filterers of organic matter (Cummins, 1993). They also serve as a primary energy link to the fish community, providing a food source for both game and forage fishes (Gore, 1989). Information from the literature (Armitage & Petts, 1992; Gore, 1994) suggests that benthic invertebrate changes will occur because of abstractions where reductions in flow have one or more of the following effects: threshold changes of hydraulics exceeded; channel bed dewatered; sedimentation of fine particulate matter; compaction of substrate sediments; development of periphyton and macrophytes; and changes in water quality. However, in a review of the impact of river regulation on invertebrate communities in the UK, Boon (1988) reported a lack of published studies on effects of abstraction.

The assessment of changes in ecosystems and especially in community composition and structure is a key question in current ecological monitoring and management. Studies of vegetation succession (eg. Van der Maarel, 1978; Van der Maarel *et al.*, 1985) have shown that ordination techniques such as Principal Component Analysis (PCA) and its many variants provide powerful tools to describe successional processes and species or community responses to environmental change (Whittaker, 1973). Assessments of the ecological impacts of river regulation have most frequently used comparisons between above- and below-reservoir locations (see Ward, 1976; Petts, 1984; Armitage, 1984; Boon, 1988 for reviews). Contrasts between the 'reference' sites and the 'impacted' ones have been investigated using various methods including similarity indices (Rader & Ward, 1988) or test procedures to assess the significance of changes in individual taxa (Extence, 1981). This paper investigates the impacts of abstraction by considering pairs of reference and impacted sites from a large-scale spatial study of UK streams (Petts & Armitage, 1991).

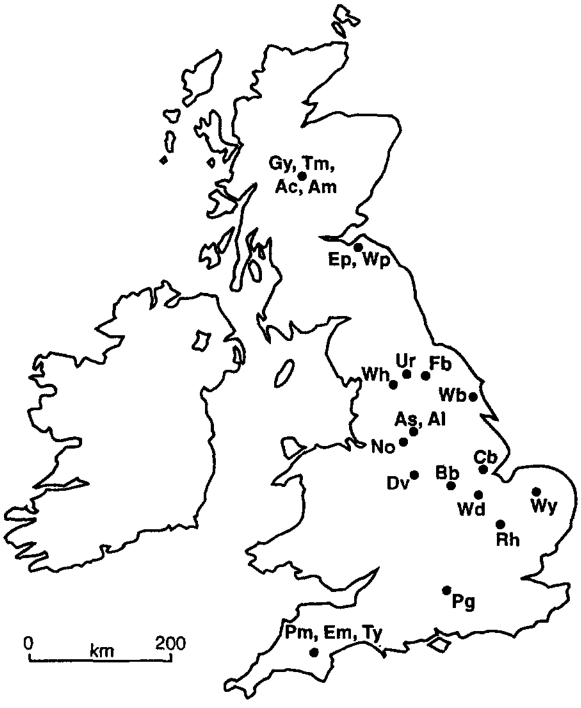

Fig. 1. The distribution of study sites in Great Britain. Allt Cuaich-Ac, Allt a'Choire Chaim-Am, Garry-Gy, Truim-Tm, Peffer East-Ep, Peffer West-Wp, Cod Beck-Fb, Ure-Ur, West Beck-Wb, Wharfe-Wh, Ashope-As/Alport-Al, Dove-Dv, Noe-No, Cringle Brook-Cb, Rhee-Rh, Welland-Wd, Wissey-Wy, Pang-Pg, Erme-Em, Plym-Pm, Tavy-Ty, Black Brook-Bb.

Sites and methods

Site selection

The faunal data collected by the Freshwater Biological Association (now Institute of Freshwater Ecology) from 370 river sites in Great Britain (Wright *et al.*, 1984) was used to facilitate the choice of a representative coverage of sites for inclusion in this study. The 23 streams selected (Fig. 1, Table 1), encompass a wide range of river types as well as incorporating examples of different types of abstraction. In terms of hydrology, the mean discharges of the selected streams range from 15 $m^3 s^{-1}$ to 0.13 $m^3 s^{-1}$ and the flow variability, defined by the Q95 as a percentage of the mean flow, ranges from over 20% on the groundwater-dominated rivers to 8% or less for rivers in the Scottish highlands. Five types of water abstraction were covered: surface-water abstractions (public water supply, hydropower production, fish farming, and spray irrigation) and groundwater abstractions.

For each abstraction, one pair of sites was investigated: one reference and one impacted. A simple pair of sites was selected because differences between riffle faunas within a single sector having uniform water-quality and geomorphology have been shown to be minimal (Furse *et al.*, 1981). Sites can be readily described and distinguished by single samples when identified to family level, a separation that may be improved with species level identification or when categories of abundance are applied to family data. The single-site methodology was employed in the development of a national prediction and classification scheme (RIVPACS) which is now in use by the National Rivers Authority (Wright *et al.*, 1989). Nevertheless, two controls were incorporated in this study: the unaffected Blackbrook, and below the abstraction on the Ashope. Each control comprised a pair of riffles having different morphological and hydraulic characteristics: one having a uniform, rectangular, cross-section and the other an asymmetric profile. The total number of pairs analysed is 31 including more than one pair on some rivers (Table 1). It should be noted that for surface-water abstractions the downstream site is impacted

Table 1. Summary of the flow data. The index of abstraction is the ratio: 'flow affected by abstraction'/'natural flow' on the day of the survey. The index of annual abstraction is: 1 - minor; 2 - moderate; 3 - major. Control pairs of sites (no abstraction) are marked *.

Stream	Code	Mean flow ($m^3 s^{-1}$)	Q95 ($m^3 s^{-1}$)	Baseflow Index (Q95/Meanflow)100	Pairs of sites	Distance between sites (km)	Index of abstraction	Index of annual abstraction
Ure	Ur	15.07	1.13	7.50	Urb-Ura	4.0	1.29	1
Wharfe	Wh	14.82	1.54	10.4	Wh2-Wh1	2.0	2.65	1
					Wh3-Wh1	4.0	2.29	1
Dove	Dv	13.88	3.73	26.9	Dvb-Dva	0.2	0.62	1
Garry	Gy	4.79	0.31	6.50	Gy2-Gy1	2.2	0.03	3
					Gy3-Gy1	5.7	0.40	3
West Beck	Wb	2.49	0.54	21.7	Wbb-Wba	1.5	0.22	2
Welland	Wd	2.40	0.22	9.20	Wdb-Wda	1.0	0.87	1
Plym	Pm	2.28	0.30	13.2	Pmb-Pma	0.2	0.81	2
Wissey	Wy	1.90	0.58	30.5	Wyb-Wya	17.5	0.07	2
Erme	Em	1.80	0.21	11.7	Emb-Ema	0.6	1.06	1
Tavy	Ty	1.78	0.26	14.6	Tyb-Tya	0.2	0.49	2
Rhee	Rh	1.25	0.27	21.6	Rhb-Rha	9.0	0.40	2
Ashope/ Alport	As/Al	1.00	0.13	13.0	As2-Al	0.5	0.36	3
					As3-Al	2.0	0.36	3
					As2-As1	0.5	0.36	3
					As3-As1	2.0	0.36	3
					As3-As2*	1.5	0.00	0
Pang	Pg	0.64	0.23	36.0	Pgb-Pga	6.0	0.03	2
Noe	No	0.59	0.08	14.0	Nob-Noa	0.5	0.50	2
Truim	Tm	0.50	0.04	8.00	Tmb-Tma	0.5	1.00	3
Allt Cuaich	Ac	0.50	0.04	8.00	Acb-Aca	0.5	0.16	3
Cod Beck	Fb	0.43	0.04	9.30	Fb2-Fb1	9.0	1.16	2
					Fb3-Fb1	14.0	2.21	2
Cringle Brook	Cb	0.33	0.09	27.3	Cbb-Cba	1.0	0.49	2
Allt a'Choire Chaim	Am	0.24	0.02	8.00	Amb-Ama	0.3	0.10	3
East Peffer	Ep	0.20	0.01	5.00	Epb-Epa	0.3	0.88	2
WestPeffer	Wp	0.13	0.01	7.70	Wp1b-Wp1a	0.1	1.00	2
					Wp2b-Wp2a	0.5	0.73	2
					Wp3b-Wp3a	0.2	1.47	2
Blackbrook	Bb				Bb2-Bb1*	0.1	0.00	0

and the upstream site is the reference but for groundwater abstractions this is reversed, the upstream site experiencing reduced flows and the downstream site providing the reference. Care was taken to locate the downstream site in the latter cases at locations where hydrological and hydraulic data indicated that a 'natural' low flow had been re-established.

The field survey was undertaken during two summers, 1989 and 1990. Because of the influence of channel width on flow hydraulics, sites were selected so that wherever possible the difference in channel width between each pair of sites was no more than ±10%. Where the abstraction involved a weir, the downstream site was chosen so as to be no less than 15 channel widths downstream to avoid any local erosional effects below the structure.

Physical habitat assessment

At each site, being a riffle or run, a sample zone was delineated by two transects 1.5 metres apart. This zone was then divided into four cells of equal width, except

Table 2. The 62 families occuring with a frequency of at least 0.02 in the 204 cells.

Family	Frequency	Family	Frequency
Planariidae	0.147	Chloroperlidae	0.127
Dendrocoelidae	0.039	Corixidae	0.074
Neritidae	0.049	Haliplidae	0.196
Valvatidae	0.083	Dytiscidae	0.299
Hydrobiidae	0.382	Hydrophilidae	0.069
Lymnaeidae	0.299	Elmidae	0.735
Physidae	0.127	Sialidae	0.167
Planorbidae	0.172	Rhyacophilidae	0.451
Ancylidae	0.265	Philopotamidae	0.074
Hydridae	0.074	Polycentropodidae	0.304
NEMATODA	0.029	Psychomyiidae	0.025
Sphaeriidae	0.431	Hydropsychidae	0.407
OLIGOCHAETA	0.843	Hydroptilidae	0.260
Piscicolidae	0.059	Limnephilidae	0.206
Glossiphoniidae	0.333	Leptoceridae	0.167
Erobdellidae	0.265	Goeridae	0.074
HYDRACARINA	0.510	Brachycentridae	0.103
Asellidae	0.314	Sericostomatidae	0.069
Gammaridae	0.412	Tipulidae	0.662
Astacidae	0.074	Psychodidae	0.088
Siphlonuridae	0.137	Ceratopogonidae	0.181
Baetidae	0.740	Tanypodinae	0.652
Heptageniidae	0.309	Diamesinae	0.289
Ephmerellidae	0.436	Prodiamesinae	0.319
Ephemeridae	0.123	Orthocladiinae	0.804
Caenidae	0.186	Chironomini	0.525
Taeniopterygidae	0.093	Tanytarsini	0.676
Nemouridae	0.270	Simuliidae	0.441
Leuctridae	0.490	Empididae	0.392
Perlodidae	0.191	Rhagionidae	0.123
Perlidae	0.147	Muscidae	0.137

for a small number of transects in which only three cells were defined because of the constraint of limited wetted area. Each cell was considered to be a distinct habitat (not a replicate) to allow comparison of marginal and mid-channel habitat, and assessment of the effect of hydraulic variability across a transect. A total number of 204 cells were investigated from the 31 pairs of sites.

Along each of the two transects, depth and velocity (at 0.6 depth) were recorded at 20 verticals at equal intervals. Thus the discharge at the time of survey was determined and each cell was defined by 10 sets of measurements. For each cell, qualitative records were also made (1) of the substrate as percentage cover of boulders/cobbles, pebbles/gravel, sand and silt/clay; (2) of the percentage cover of macrophytes; and (3) of the presence or absence of detritus. Also for each site 1:25000 maps were examined to determine distance from source, altitude and channel slope. Water-quality data (conductivity, nitrite, nitrate, chloride and alkalinity) were obtained either from water samples collected during the survey or from the appropriate water undertaking.

Biological assessment

Macroinvertebrate samples were obtained from each cell by means of a timed (1.5 minute) kick method (Armitage *et al.*, 1974) using a net (230×255 mm frame, 90 μm mesh). The relatively small size of the cells precluded the use of the kick-and-sweep technique used in Furse *et al.* (1981), but taken together they provide the equivalent in terms of sampling effort and area covered. Individual cell values can be regarded as providing a measure of replication and minimum estimates of the faunal parameters. The invertebrate samples represent catch per unit effort and because they were taken in a standard way can be used to provide estimates of relative abundance of taxa (Armitage *et al.*, 1974). Faunal samples were preserved in 5% formaldehyde solution, sorted into 70% alcohol and identified to species level where possible. Chironomidae and Oligochaeta were taken to sub-family/tribe and family level respectively. Hydracarina were recorded as such. Only the family data will be considered for the main analyses in the present paper. Species data have not been considered here, but the same series of analyses as described herein for the family data led to the same conclusions (Petts & Armitage, 1991).

The analysis of change

An approach was developed based upon the differences between pairs of samples, following Beffy (1989). Data processing was divided into three successive steps using various multivariate analyses to achieve specific objectives, as summarized in Fig. 2. All data processing has been carried out using the ADE program ('Analyse des Donńees Ecologiques') of D. Chessel, J. Thioulouse, J. L. Beffy & Y. Auda (PIREN-Vallées Fluviales, URA CNRS 367, Université Lyon 1, France). Graphical outputs from the numerical analyses have been generated using the GraphMu programme of Thioulouse (1989) which is interfaced with ADE.

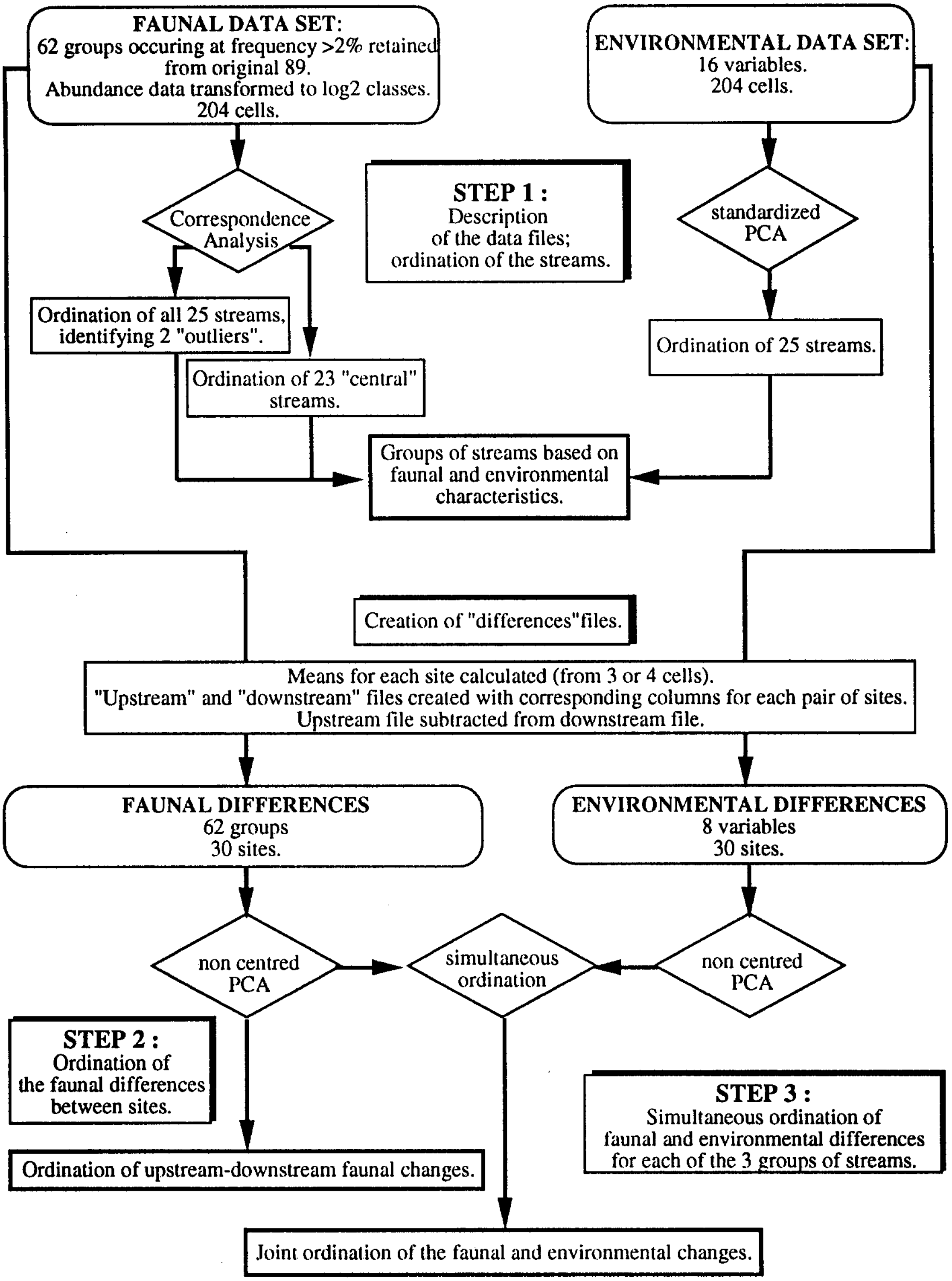

Fig. 2. **Flow diagram summarizing the approach used for data analysis.**

Table 3. Eigen values and correlation values for the first axis of the separate and simultaneous ordinations of the environmental variables and faunal data.

	1 Eigen values from the separate ordinations		2 Eigen values from the simultaneous ordination		3 Ratio 2/1		4 Correlation between the simultaneous ordinations of the fauna and the variables
	Variables	Fauna	Variables	Fauna	Variables	Fauna	
Upland streams	2.23	64.72	1.99	33.19	0.89	0.51	0.59
Intermediate streams	3.77	131.6	3.35	79.57	0.89	0.60	0.88
Lowland streams	7.54	109.8	7.00	101.0	0.93	0.92	0.91

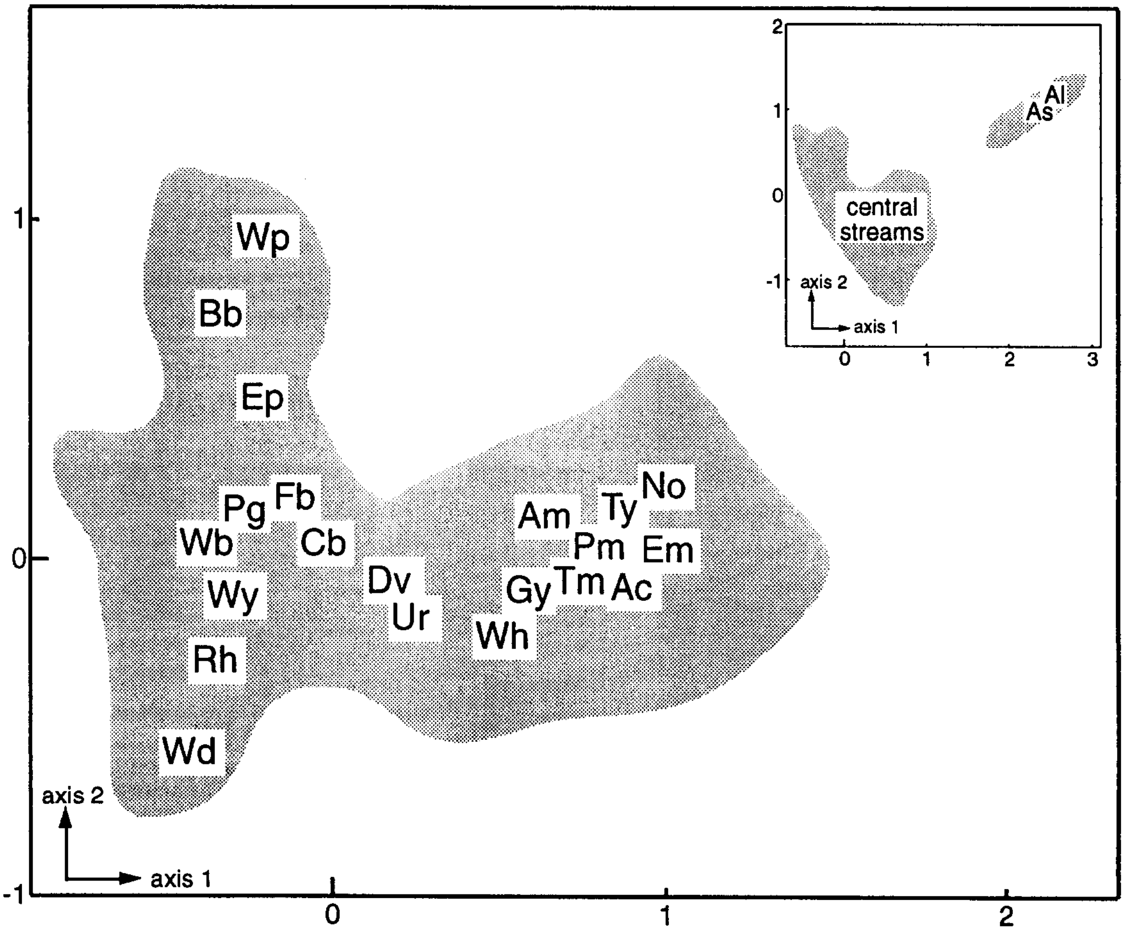

Fig. 3. Ordination of the family data-set using Correspondence Analysis. The abbreviations of the streams are listed in Table 1. Abbreviations are located at the centre of gravity of the cells (points). Insert shows the ordination of the original family data set (204 cells, 23 streams, 62 families). The main figure shows the ordination of the central cluster of streams (188 cells, 21 streams, 62 families).

Description of the faunal and environmental data sets

In order to assess between-site and within-site (between cell) variations, separate analyses, using the appropriate multivariate ordination methods, were performed (a) on the 'faunal data set' – data from 204 cells, simplified by removing the less frequent taxa (occurring in less than 2% of cells), and transforming abundances to log2 classes; and (b) the 'environmental data set' – values of 16 variables from the same 204 cells. Table 2 lists the taxa included in the simplified faunal data set with their cell frequencies.

Correspondence Analysis (CA) was used to analyse the faunal data set. CA was chosen instead of its detrended version (DCA) which has been used in many studies for several reasons: (i) the arch effect, which detrending is intended to eliminate, can be regarded as an accurate representation of the data and confirms the existence of a strong unidimensional gradient (Van Der Maarel, 1980; Wartenberg *et al.*, 1987; Minchin, 1987); (ii) control over the geometry is lost in the process of detrending and DCA breaks up the optimal properties of CA such as the maximisation of correlations or the reciprocal averaging (Greenacre, 1984; Lebreton and Yoccoz, 1987); (iii) DCA is an *ad hoc* and arbitrary adjustment of CA and lacks mathematical coherency (Wartenberg *et al.*, 1987; Minchin, 1987; Lebreton & Yoccoz, 1987), hence it does not allow subsequent 'inter-battery analyses'.

For the environmental data set, a standardised Principal Components Analysis (PCA) was used, this being most suitable for data where each sample is scored for the same set of variables and differences between samples are 'quantitative', i.e. where differences are defined in terms of the 'magnitude' of the variables. In a Standardised PCA the variables are first standardised so that each has the same range. This is necessary where variables have different units of measurement. The resulting ordination diagram describes the relationships of the 204 cells based on the values and inter-correlations of the 16 variables.

Analysis of differences

This second step involved analysis of the 'differences' in the fauna and environmental variables between the pairs of sites. Files of differences describing the actual changes in faunal abundances and values of environmental variables between the upstream and downstream sites were constructed (Fig. 2, step 2), with negative values indicating decreases and positive values increases at the downstream sites. A non-centred PCA (NPCA) was performed on the differences file to detect any quantitative changes. The inclusion of both positive and negative values in the 'differences' excluded the use of CA or DCA for comparing the directions and amplitudes of changes.

Each difference between impacted and reference sites can be considered as a vector. The NPCA provides an ordination of all these vectors, i.e. an ordination of changes and allows comparison of the amplitude of the changes (i.e. the length of the vectors) as well as of their trend or direction (i.e. the orientation of the vectors). Projection of the original data for the upstream and downstream sites as supplementary points in the ordination (Cazes, 1982a, b) allows comparison of the two states of each site (indicated by the relative distances between the vectors on the factorial planes – see Beffy (1989) for a mathematical development).

Simultaneous ordination of the faunal and environmental changes

The final stage of the analysis was performed to describe any common patterns in the faunal and environmental changes. The method seeks to match the ordination of two data sets sharing the same set of measurements or samples, and to identify common structures. This 'co-inertia analysis' (Mercier, 1991; Chessel & Mercier, 1993) has been used as 'inter-battery analysis' by Bornette *et al.* (in press). The method generates factorial axes and axis scores for both the individuals (e.g. the samples) and the variables (e.g. species or environmental parametres) of the two matched tables. The factorial axes are sought here in order to maximize simultaneously (i) the variance of the axis scores for the first data set, (ii) the variance of the axis scores for the second data set, and (iii) the covariance between these two sets of axis scores. The advantage of simultaneous ordination is that it allows the matching of two data sets with their own appropriate ordination technique.

Simultaneous ordination of the two data files (the environmental and the faunal differences files) provides four sets of ordination scores: (1) the axis scores for the environmental variables, (2) the axis scores for the faunal groups, (3) the axis scores for the pairs of sites (differences) based upon the environmental variables and (4) the axis scores for the pairs of sites (differences) based upon the fauna. The similarity between the ordinations obtained in (3) and (4) (i.e. the correlation between the scores for each factorial axis) expresses the strength of the relationship between the environmental and the faunal changes. Furthermore, for each of the two data sets and each factorial axis, the ratio between the eigen value calculated in the simultaneous ordination and the eigen value calculated in a normal ('separated') ordination, is a measure of the amount of between-sample variation explained by the other data set (i.e. the closeness with which the ordering of the samples based on the faunal data set resembles that based on the environmental data set). From the many possible ways of displaying these numerical outputs, we chose to use the four sets of factorial scores to rearrange the original files of environmental and faunal differences.

Results

Site description and regional-scale analysis

Ordination of the whole data set (204 cells and 62 taxa) describes on the first two axes the peculiarity of two rivers (Fig. 3.1): the Ashope and Alport. These outliers have rather specialist faunas with few taxa in common with the other rivers. In order to discriminate more clearly between the cells in the central cluster, the Correspondence Analysis was repeated after removing the data for the 16 cells from the two outlying streams. This achieved a better scattering of the 21 remaining streams, displaying a strong between-stream structure (Fig. 3.2).

The ordination was used to group the streams into three sets by considering the position of the centre of gravity of the cells belonging to each stream on the first axis. The three sets are: (1) typical upland streams, (2) typical lowland streams, and (3) an intermediate set including the middle reaches of large upland rivers (Wharfe-Wh, Dove-Dv, Ure-Ur) and two lowland gravel-bed streams (Cod Beck-Fb, Cringlebrook-Cb) the fauna of which has features intermediate between the two 'typical' sets. The second axis introduces a secondary distinction within the lowland set, contrasting the Welland, Rhee and Wissey (lowland streams) with the Peffers and Blackbrook (impoverished lowland streams).

Examination of the mean abundances of the faunal groups for each stream confirms the regional groupings. To illustrate the faunal basis of the ordination we chose the insect groups (excluding Diptera), which proved to be sufficiently diverse to provide a picture of the faunal differentiation between the types of streams (Fig. 4). In this figure, the families as well as the streams are ranked according to their first axis scores in the Correspondence Analysis. 'Faunal profiles' obtained for each stream are grouped according to the sets depicted in the ordinations. The progressive shift in the occurrences and abundances of the faunal groups explains the grouping of the streams.

The peculiarity of the Alport (Al) and Ashop (As) is explained by the occurrence of a set of lotic insect families, especially stoneflies, and by the lack, or the very low abundance, of most of the 'non insect' groups and Diptera. The upland streams (Noe-No to Garry-Gy) are characterized by families 19 (Heptageniidae) to 29 (Taeniopterygidae), whereas families 1 (Corixidae) to 14 (Ephemerellidae) dominate in the lowland streams (Pang-Pg to Welland-Wd). The intermediate set of streams (Wharfe-Wh to Cod Beck-Fb) is characterized by an intermediate spectrum. The Peffers (Wp and Ep) and Blackbrook (Bb) exhibit an impoverished lowland-type spectrum and harbour mostly Diptera (Tanytarsini, Orthocladiinae, Prodiamesinae, Tanypodinae), Oligochaeta and Sphaeriidae.

Ordination of the 204 cells according to the 16 environmental variables on the first axis of the PCA describes a strong between-streams structure (Fig. 5). The distribution of sites on this axis explains the distinction between upland and lowland streams in a predictable way. Coarse substrate, altitude and slope are positively correlated with the axis 1 ordination scores (high values in the upland set), whereas fine sediment, alkalinity, chloride and detritus are negatively correlated with these scores (high values in the lowland set). Discharge and the hydraulic variables are not correlated with the axis 1 scores. The information provided by the second axis is of minor importance (explaining only a small proportion of the variation in the data) and is mostly concerned with discriminating some cells on the Dove (Dv) and the Wissey (Wy) characterized by high velocity.

At this stage of the analysis regional differences clearly dominate over local effects and the impact of abstraction. The strong upland-lowland contrast is obviously the dominant structure within both the faunal and environmental data.

Ordination of differences between reference and impacted sites

The ordination of the faunal changes according to the first four axes of the NPCA shows a high level of heterogeneity. In Fig. 6.1 the arrows represent the faunal

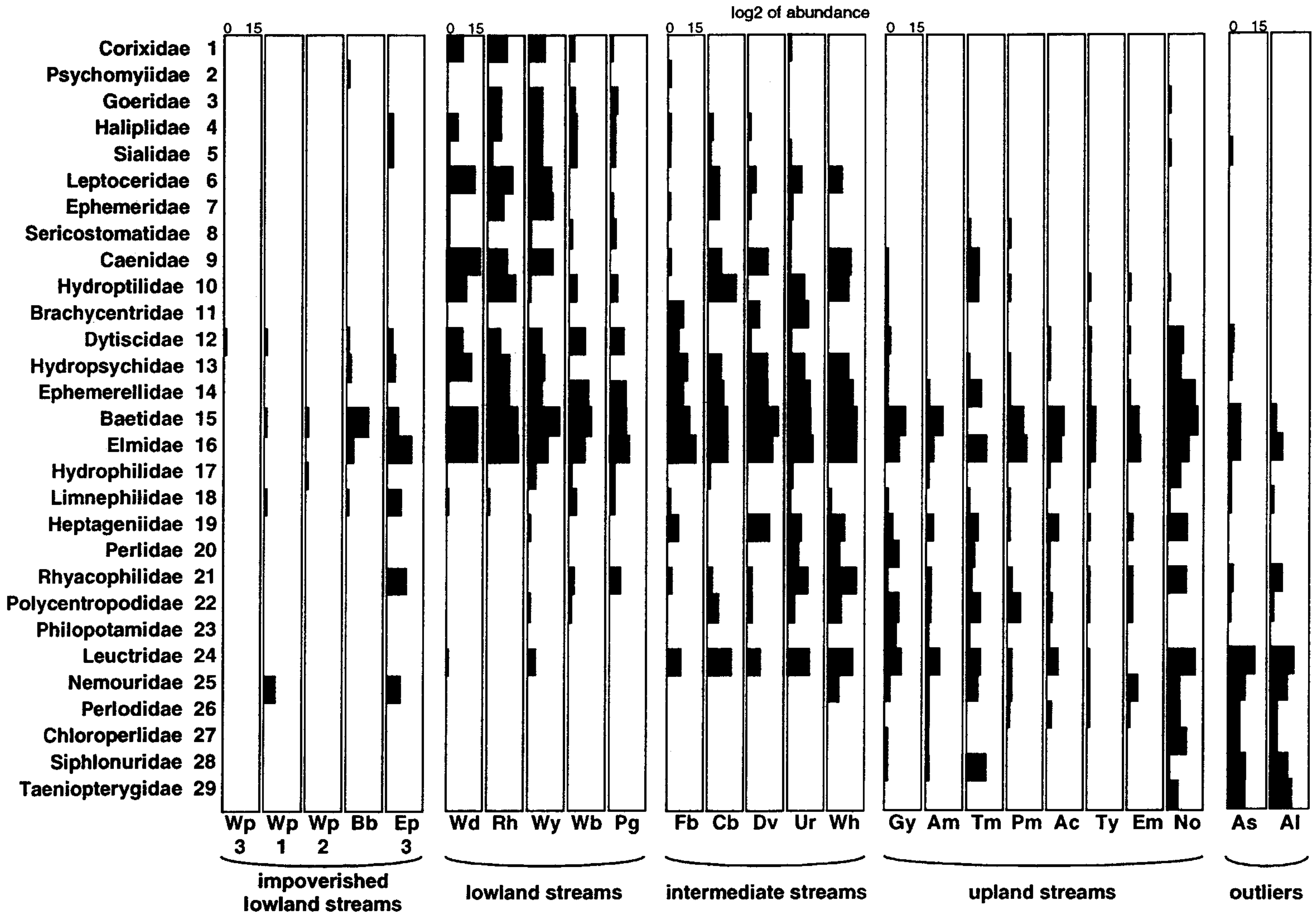

Fig. 4. Mean abundances per stream ($\log_2$ transformed) of the insects except Diptera. The streams and the taxa are ranked according to their score in the Correspondence Analysis.

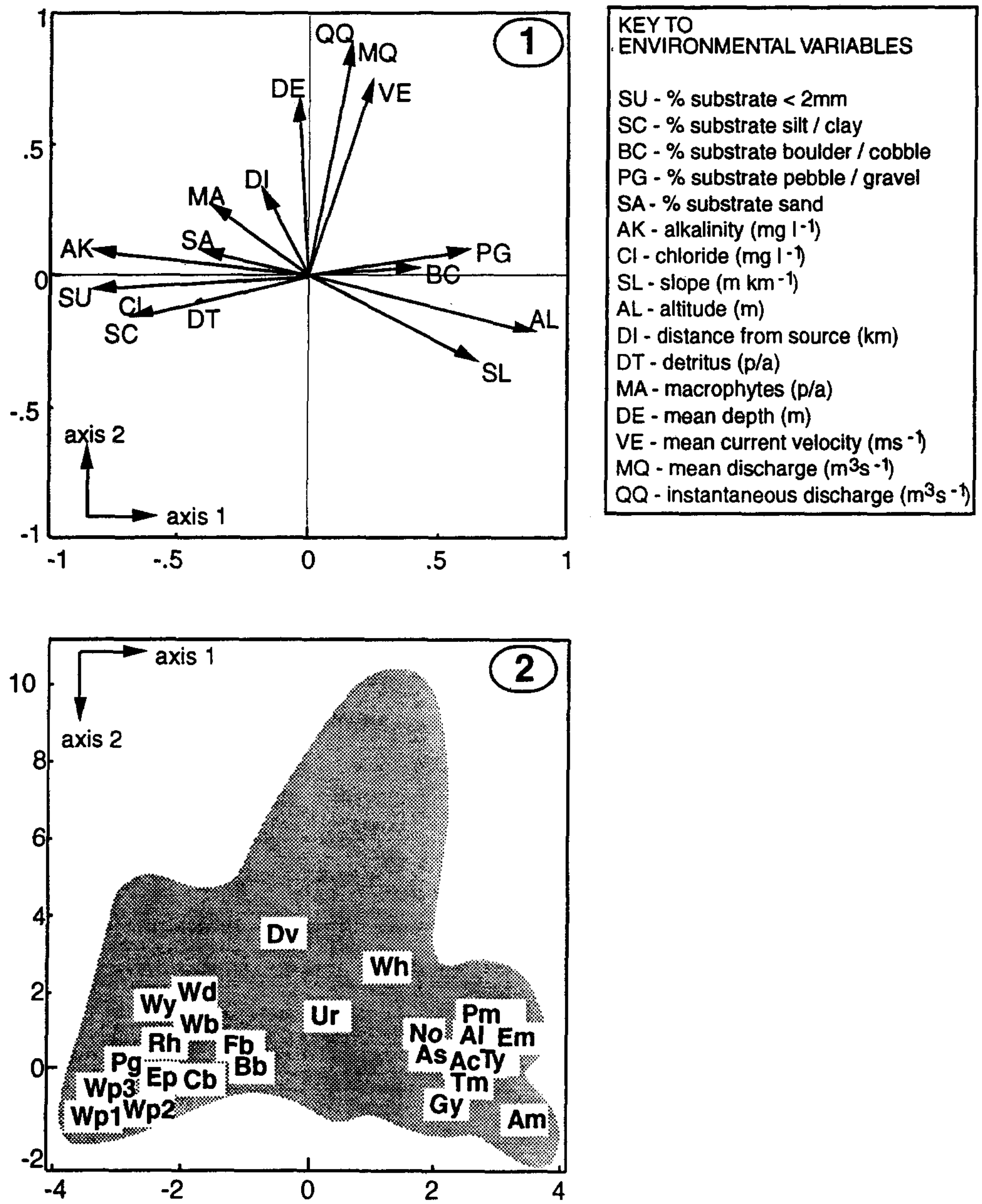

Fig. 5. Ordination of the environmental variable data using standardised PCA. The abbreviations of the streams are listed in Table 1. Abbreviations are located at the centre of gravity of the cells (points). 1. Ordination of the 16 variables. 2. Ordination of the 204 cells.

differences between the impacted and reference sites. The changes occur in all directions and with all degrees of magnitude but is important to note that the two control pairs have similar faunas. To investigate patterns of differences within and between groups of sites, sites have been classified according to stream type (defined above) and intensity of abstraction. The second criterion is a qualitative evaluation of the annual intensity of abstraction assessed from the available information on the licensed or actual abstractions (Table 1). The abstractions considered as 'minor' tend to be associated with low faunal changes, but within the 'moderate' and 'major' types of abstractions large differences (Wissey, Rhee, Pang, Garry, Truim, Cod Beck, Cringle Brook) coexist with insignificant ones (Tavy, Plym, West Peffer, Ashope, Allt a'Choire Chaim, Allt Cuaich). Furthermore, there is an obvious lack of consistency in the orientation of the changes within any one given group. The ordination of the faunal changes according to the third and fourth axes did not reveal any more coherent relationships.

Other groupings were also investigated based on a baseflow index (mean discharge divided by the 95th percentile flow, Q95) and an index of abstraction on the day of sampling (ratio between the discharges at the impacted and reference sites) (Table 1). However, the pattern of changes defined by the analysis could not be clarified.

The final step of the analysis aimed to describe relationships between the faunal and the environmental changes for each pair of sites. A simultaneous ordination of the environmental and faunal differences was run separately for the three types of streams (upland, intermediate, lowland) in order to reduce the influence of regional differences. Only eight environmental variables were retained, those being considered to be closely related (directly or indirectly) to the effects of water abstraction: discharge, depth, velocity, siltation (indexed by the proportion of sand, silt/clay and sub-sand), detritus accumulation, and the influence of macrophytes. A file containing the differences for each of the variables and for each pair of sites was calculated as indicated for the faunal data but following a standardization of each variable.

Examples of the upland and lowland streams (Figs 7 and 8) show the variables, the taxa and the pairs of sites arranged according to their score on the first axis of the simultaneous ordinations. For one given faunal group or variable, the change between the reference and impacted sites is represented as a square (decrease) or a circle (increase), the surface area of which is proportional to the value of the change. These diagrams provide a graphical synthesis of the changes for the different pairs of sites. The eigen values and correlations for the three analyses (Table 3) point to a difference in the amount of co-variation between environmental and faunal differences for the three sets of streams. The strength of the relationship appears to be highest in the lowland set (0.91) and lowest in the upland set (0.59). These values are illustrated in the closer similarity between the two F1-ordinations of the sites in the lowland set (Fig. 8) than in the upland set (Fig. 7).

In the upland group, between-site faunal differences are related to differences of the environmental variables in some cases only. For example, major changes occur in the Garry (Gy) and the Truim (Tm), but in opposite directions. In particular, a set of Diptera (Diamesinae, Tanypodinae, Orthocladiinae, Tanytarsini) and also Polycentropodidae, Oligochaeta and Elmidae, which increase in the Truim, tend to decrease in the Garry. This ordination of the faunal changes is loosely correlated with the changes in the environmental variables. For example, the Truim does not show any important changes in the environmental variables, whereas the sites on the Garry exhibit more noticeable changes, especially a decrease in velocity. Furthermore, on the Ashope (As) where major environmental differences occur between the reference and impacted sites, this is not reflected by the fauna.

In the lowland group, the major changes occur in the three streams affected by groundwater abstraction (Wissey-Wy, Rhee-Rh, Pang-Pg). There are several common points between the three groundwater-affected sites. Note that in these streams, the impact occurs at the upstream site resulting from a lowering of the water-table due to groundwater pumping. These rivers share a set of taxa that mainly decrease in abundance from the reference to the impacted sites (from Physidae to Piscicolidae at the upper part of the table). They also exhibit important changes in environmental variables such as a decrease in depth and macrophytes. The Wissey exhibits both the greatest environmental changes and the clearest faunal impacts. There are some inconsistent differences, for example the taxa in the lower part of the table tend to decrease at the impacted site on the Pang, whereas they increase at the impacted site on the Rhee and the Wissey. Nevertheless, the ordination of the faunal changes is more highly correlated with the differences in the variables than in the case of the upland group.

Discussion

The preliminary description of the family and environmental data sets using multivariate ordination methods stressed the strength of the between-stream differences in the total variability of the data set at the individual-cell level. This was related to the expected differences between upland and lowland streams (Wright *et al.*, 1984) and led to a grouping of the streams into three types (upland, intermediate, lowland) based on the family data and supported by the environmental variables. This result, together with the similarity between the reference and impacted sites at this level of analysis,

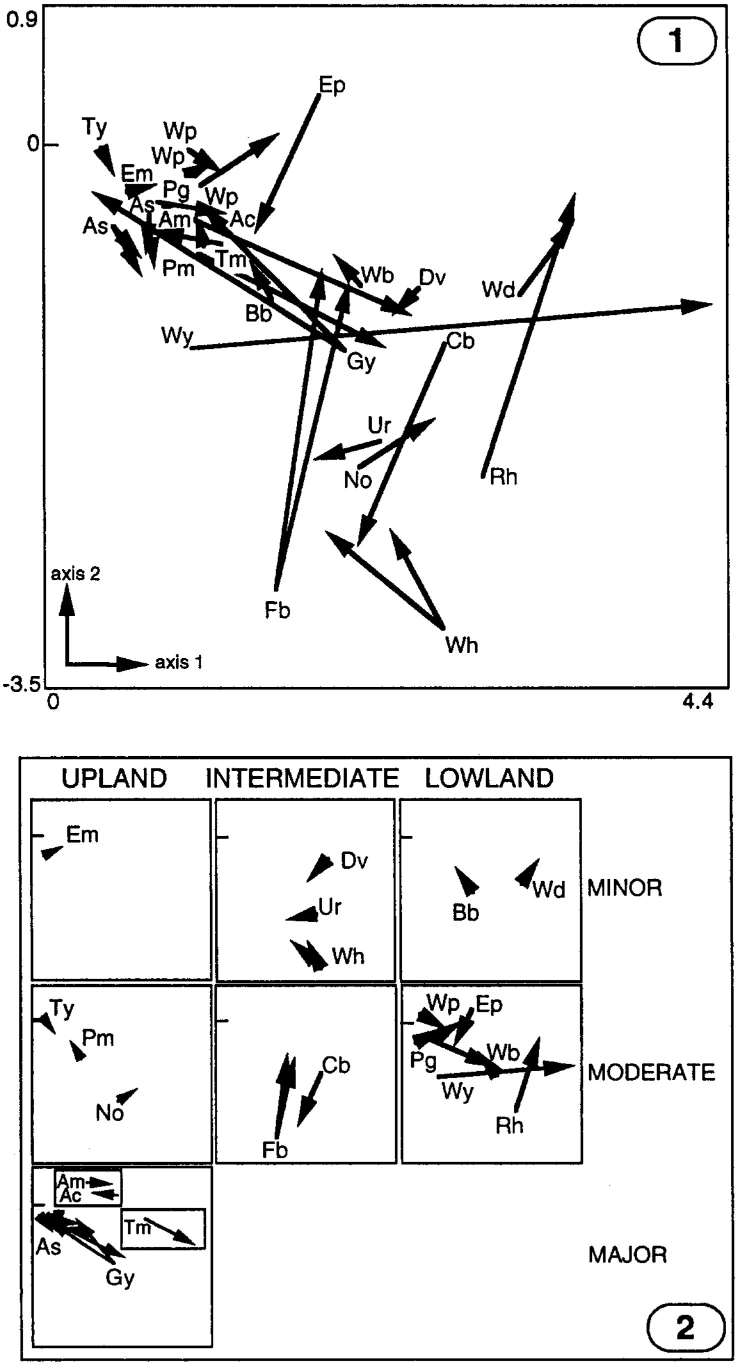

Fig. 6. Ordination of the changes of the family data (non-centred PCA). The vectors are orientated from upstream to downstream. 1. F1 × F2 ordination. 2. Separation of the F1 × F2 ordination according to the type of stream and an overall estimation of the impact of abstraction (see Table 1).

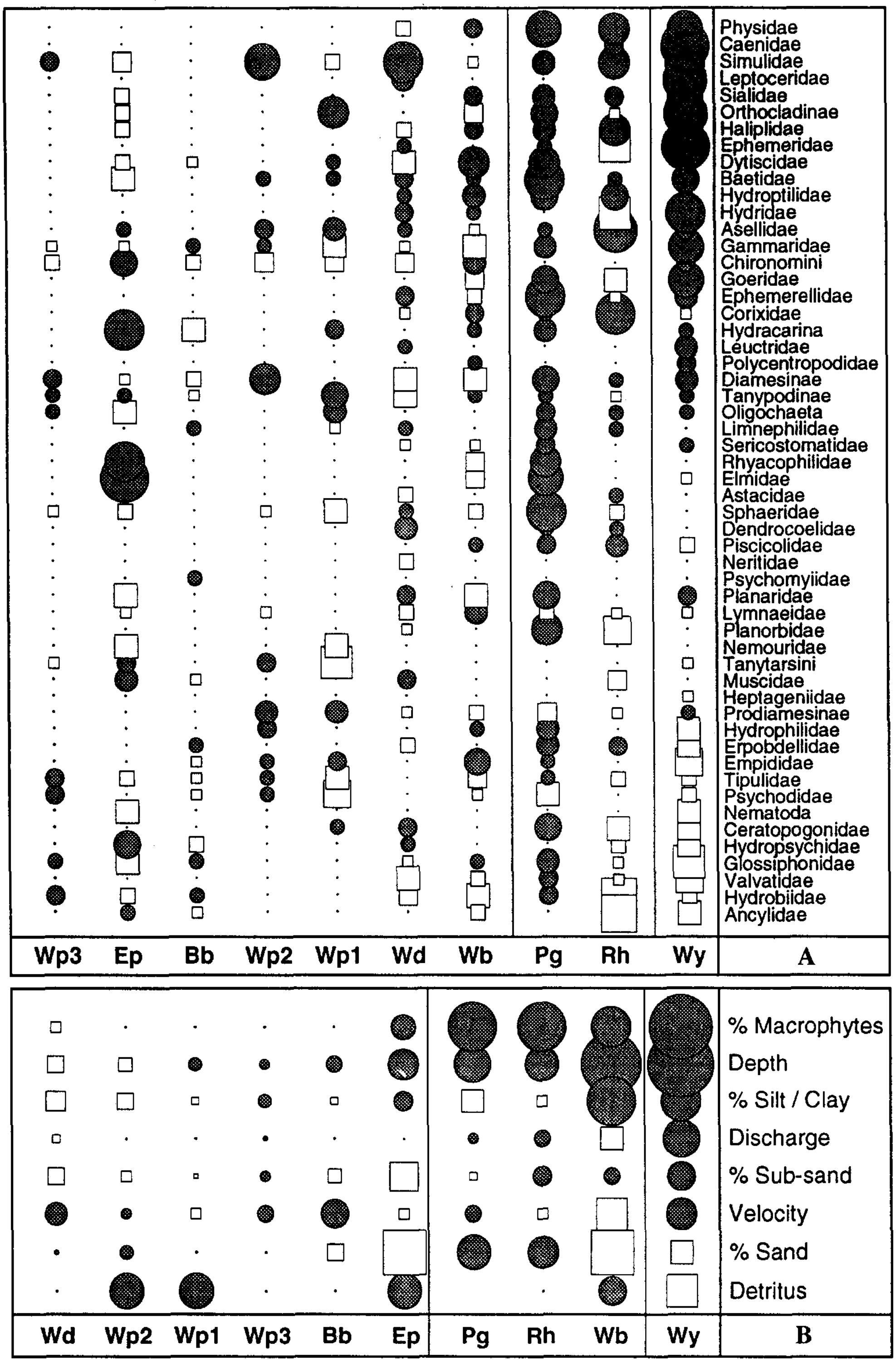

Fig. 7. Simultaneous ordination of the faunal changes (family data) and of the environmental variable changes for the upland set of streams. The circles represent increases of faunal abundance or of the value of the variable from upstream to downstream, whereas squares represent decreases. The areas of the squares and circles are proportional to the difference between sites. The taxa, the variables and the pairs of sites are ordinated according to their scores on the first axis of the simultaneous ordination. The vertical lines indicate the major partitions depicted by this first axis.

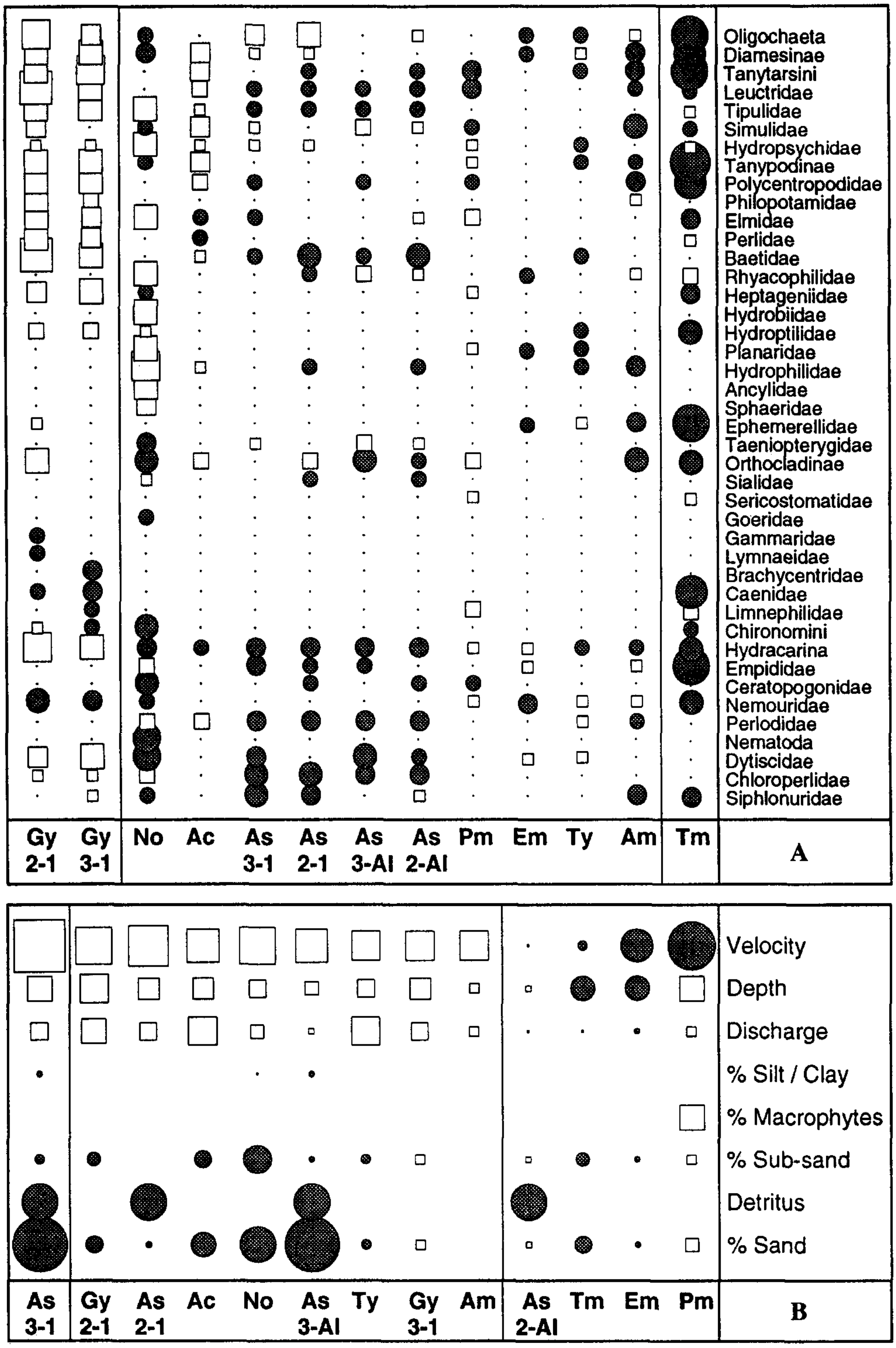

Fig. 8. Simultaneous ordination of the faunal changes (family level) and of the environmental variable changes for the lowland set of streams. Upstream to downstream changes of faunal abundance and environmental variable are represented by circles (increases) or squares (decreases). Note that in most cases the impacted site is downstream but for the rivers affected by groundwater abstraction the impacted site is upstream (Wy, Pg and Rh). The areas of the squares and circles are proportional to the absolute value of the difference between sites. The taxa, the variables and the pairs of sites are ordinated according to their scores on the first axis of the simultaneous ordination. The vertical lines indicate the major partitions depicted by this first axis.

emphasized the need for a specific approach to isolate and evaluate the influence of water abstraction.

The two pairs of control sites were shown to have similar faunas. This supports the accepted view that local site factors are relatively unimportant in determining invertebrate faunas (Furse, *et al.*, 1991) although faunal differences have been attributed to riffle type in small streams (Petts & Armitage, 1993). The analysis of data for the impacted rivers failed to demonstrate any coherent changes in amplitude or orientation of the faunas either in relation to the type of abstraction, intensity of abstraction, or the type of stream.

Differences between reference and impacted sites that may be attributed to abstraction were clearly defined in four cases: the Garry, Wissey, Rhee, and Pang. A relatively small group of environmental factors characterise these sites; factors indicating the importance of site-specific and threshold hydraulic conditions. Changes of the invertebrate community occurred where in all cells at the impacted site mean flow velocity was less than 0.05 m s^{-1} and mean depth was less than 10 cm. A marked reduction in macrophyte cover and an increase in the proportion of fine sediments were typical of the lowland groundwater impacted sites.

Of the upland streams, the River Garry had a markedly reduced fauna, and can be regarded as a good example of a large upland stream whose flow has been substantially affected by abstractions for power generation. The case of the Truim, the other upland stream exhibiting important changes, is difficult to interpret, most of the taxa increasing in abundance at the impacted site. However, the fact that some rheophilous taxa such as Hydropsychidae do decrease from the reference to the impacted site, could provide evidence of the effects of abstraction.

The lack of more conspicuous effects of even large-scale abstractions on macroinvertebrates in other upland rivers such as the Allt Cuaich, the Allt a'Choire Chaim, the Ashope/Alport or the Tavy may relate to three environmental factors: (1) upland rivers are naturally characterised by a high flow variability within and between years, and the invertebrate community may be adapted, within limits, to extreme flow conditions; (2) within gravel-bed, riffle-pool, rivers even under extreme low-flow conditions, moderate flow velocities may be maintained especially within asymmetric cross-sections, albeit within a reduced area of channel bed, to sustain the fauna; and (3) the drainage density of upland rivers in Britain is high, the main river being frequently joined by small tributaries and faunal drift from these, together with drift along the mainstream during frequent spates, may lead to the rapid, and repeated, recolonization of sites impacted by abstraction.

Concerning the lowland group, the streams affected by groundwater abstraction appeared to be the most consistently degraded. Faunal decreases at impacted sites appear to be more closely correlated with the changes in the environmental variables than in the case of the upland streams. Although differences between sites on rivers affected by groundwater abstraction may relate to the downstream distance between sites (see Bickerton *et al.*, 1992), it may be proposed that invertebrate communities of lowland streams, with a more naturally regulated discharge pattern, might be particularly sensitive to extreme low flows.

The faunal aspects of these results will be developed and elaborated in another paper, but it can be stressed that the taxa which appeared in this study to be exhibiting the largest changes, such as the Baetidae, Chironomidae, Hydropsychidae, Gammaridae and Simuliidae are also those most frequently mentioned as being significantly affected by reduced or intermittent flow conditions and drought (Ladle & Bass, 1981; Extence, 1981; Wright *et al.*, 1984; Wright & Berrie, 1987; Weisberg *et al.*, 1990). Furthermore, the extensive character of this study and the large variability of faunal responses it highlights, help to place the above single-case studies within the overall picture of a multiplicity of possible trends in faunal responses to reduced flow conditions.

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References

Armitage, P. D., 1984. Environmental changes induced by stream regulation and their effect on lotic macroinvertebrate communities. In Lillehammer, A. & S. J. Saltveit (eds), Regulated Rivers, Oslo University Press, Norway: 139–165.

Armitage, P. D., A. M. Machale & D. C. Crisp, 1974. A survey of stream invertebrates in the Cow Green basin (Upper Teesdale) before inundation. Freshwat. Biol. 4: 369–398.

Armitage, P. D. & G. E. Petts. Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. Aquat. Conserv. 2: 1–18.

Beffy, J. L., 1989. L'analyse en composantes principales d'un nuage de vecteurs: son usage pour décrire l'évolution d'un écosystème aquatique. DEA Report, Laboratoire d'Ecologie des Eaux Douces, Université de Lyon 1, F-69622 Villeurbanne Cedex, France.

Bickerton, M., G. E. Petts, P. D. Armitage & E. Castella, 1993. Effects of groundwater abstraction on the ecology of chalk streams. Regulated Rivers 8: 121–134.

Boon, P. J., 1988. The impact of river regulation on invertebrate communities in the U.K.. Regulated Rivers 2: 389–409.

Bornette, G., C. Amoros & D. Chessel. Rejuvenation in former braided channels of the Rhone River: successional patterns and allogenic processes. J. Vegetat. Sci. in press.

Cazes, P., 1982a. Note sur les éléments supplémentaires en analyse des correspondances. I Pratique et utilisation. Les Cahiers de l'Analyse des données 7: 9–23.

Cazes, P., 1982b. Note sur les éléments supplémentaires en analyse des correspondances. II Tableaux multiples. Les Cahiers de l 'Analyse des données 7: 133–154.

Cummins, K. W., 1993. Invertebrates. In Calow, P. & G. E. Petts. Rivers Handbook Blackwell Scientific, Oxford: 234–250.

Extence, C. A., 1981. The effect of drought on benthic invertebrate communities in a lowland river. Hydrobiolgia 83: 217–224.

Furse, M. T., J. F. Wright, P. D. Armitage & D. Moss, 1981. An appraisal of pond-net samples for biological monitoring of lotic macroinvertebrates. Wat. Res. 15: 679–689.

Gore, J. A., 1989. Models for predicting benthic macroinvertebrate habitat suitability under regulated flows. In Gore, J. A. & G. E. Petts. Alternatives in Regulated River Management. CRC Press, Boca Raton, Florida: 253-266.

Gore, J. A., 1994. Hydrological change. In Calow, P. & G. E. Petts. The Rivers Handbook. Blackwell Scientific 2: 33–54.

Greenacre, M. J., 1984. Theory and applications of Correspondence Analysis. Academic Press. 363 pp.

Ladle, M. & J. A. B. Bass, 1981. The ecology of a small chalk stream and its responses to drying during drought conditions. Arch. Hydrobiol. 90: 448–466.

Lebreton, J. D. & N. Yoccoz, 1987. Multivariate analysis of bird count data. Acta Oecologica, Oecol. Gener. 8: 125–144.

Mercier, P., 1991. Analyse des relations espèces-environment et étude de la co-structure d'un couple de tableaux. Doctoral Thesis, University of Lyon, 168 pp.

Mercier, P. & D. Chessel. A new method to explore species-environment relationships. An application in plant ecology. in press.

Minchin, P. R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89–107.

Petts, G. E. & P. D. Armitage, 1993. Physical habitat changes and macroinvertebrate response to river regulation: the River Rede, UK. Regulated Rivers 8: 167–178.

Petts, G. E., 1984. Impounded Rivers. Wiley, Chichester.

Petts, G. E. & P. D. Armitage, 1991. Effects of abstraction on invertebrate communities in UK rivers. Nature Conservancy Council, Peterborough, 3 volumes.

Rader, R. B. & J. V. Ward, 1988. Influence of regulation on environmental conditions and the macroinvertebrate community in the Upper Colorado River. Regulated Rivers 2: 597–618.

Ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 69: 69–77.

Thioulouse, J., 1989. Statistical analysis and graphical display of multivariate data on the MacIntosh. Computer Applications in the Biosciences 5: 287–292.

Townsend, C. R., A. G. Hildrew & K. Schofield, 1987. Persistence of stream invertebrate communities in relation to environmental variability. J. anim. Ecol. 56: 597–613.

Van der Maarel, E., 1980. On the interpretability of ordination diagrams. Vegetatio 42: 43–45.

Van der Maarel, E., 1978. Experimental succession research in a coastal dune grassland, a preliminary report. Vegetatio 38: 21–28.

Van der Maarel, E., R. Bost, D. Van Dorp & J. Rijntjes, 1985. Vegetation succession on the dunes near Oostvoore, The Netherlands; a comparison between 1959 and 1980. Vegetatio 58: 137–187.

Ward, J. V., 1976. Effects of flow patterns below large dams on stream benthos: a review in Orsborn, J. F. & C. H. Allman (eds). Instream flow needs Symposium, vol. 2, American Fisheries Society, Bethesda, Maryland, USA: 235–253.

Wartenberg, D., S. Ferson & F. J. Rohlf, 1987. Putting things in order: a critique of detrended correspondence analysis. Am. Nat. 129: 434–448.

Weisberg, S. B., A. J. Janicki, J. Gerritsen & H. T. Wilson, 1990. Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam. Regulated Rivers 5: 265–277.

Whittaker, R. H. (ed.), 1973. Ordination and classification of communities. Handbook of vegetation science 5: 737 pp.

Wright, J. F., D. Moss, P. D. Armitage & M. T. Furse, 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. Freshwat. Biol. 14: 221–256.

Wright, J. F. & A. D. Berrie, 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. Regulated Rivers 1: 145–160.