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Epilithic diatoms in Welsh lakes and streams

T.E.H. Allott & R.J. Flower

Final Report to the Welsh Office

on Contract No. PAE 22-01-004

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Environmental Change Research Centre

University College London

26 Bedford Way

London

WC1H 0AP

Executive Summary

1. This is the final report to the Welsh Office under contract PAE 22-01-004: Acid Waters Survey - Diatom Analysis.
2. 236 epilithic diatom samples have been analysed from the 104 stream sites and 32 lake sites included in the 1995 Welsh Acid Waters Survey. Sampling methodologies followed those of the Acid Waters Monitoring Network, and diatom taxonomy and nomenclature follows the Surface Waters Acidification Project (SWAP).
3. Multivariate data analyses have been used to;
 - (i) describe the variation in diatom assemblages in the stream and lake sample datasets;
 - (ii) explore the relationships between the diatom assemblages and site-specific environmental variables.
4. Species composition of the stream sample assemblages is strongly related to stream-water alkalinity and co-variables. There are also significant but less pronounced relationships between the diatom assemblages and (i) stream-water Fe concentrations, (ii) catchment variables representing stream-water flow and current velocity conditions, and (iii) sampling period. The stream samples have been classified into 10 assemblage groups which reflect a gradient of stream-water alkalinity. These groups have been described in terms of species composition and environmental characteristics.
5. Variation in species composition within the lake sample assemblages is most strongly related to lake-water pH and co-variables. The lake dataset is small, and further environmental influences on the diatoms are difficult to identify with confidence. The lake sample dataset has been classified into six assemblage groups, which reflect variation in lake-water acidity.
6. Slides from all samples have been archived at the Environmental Change Research Centre, University College London, the Natural History Museum, and the National Museum of Wales.
7. The epilithic diatom datasets described in this report provide an important resource for (i) comparison with other chemical and biological components of the 1995 Welsh Acid Waters Survey, and (ii) potential comparison with future change in diatom assemblages at the survey sites.

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1 Introduction

This report presents results from the diatom component of the 1994/95 Welsh Acid Waters Survey, incorporating 120 lake and stream sites. Diatom assemblages in upland surface waters are strongly related to surface water acidity (e.g. Charles 1985, Flower 1986, Stevenson *et al.* 1991, Juggins 1992) and epilithic diatoms potentially provide a powerful ecological tool for monitoring and assessing freshwater acidification (e.g. Patrick *et al.* 1995, Lancaster *et al.* 1996). Although epilithic diatoms were not sampled in the first Welsh Acid Waters Survey in 1984, and are therefore not available for comparative purposes, samples were taken in the recent survey to (i) establish the patterns of variation in epilithic diatom assemblages for comparison with other chemical and biological components of the survey and (ii) provide a dataset for comparison with possible future surveys. This report describes the epilithic diatom assemblages in both the stream and lake samples, and relates the assemblage variation to site-specific environmental data. The data analytical strategy is broadly based on Juggins (1992) analyses of the Scottish Baseline Survey epilithic diatom dataset.

2 Methods

2.1 Field sampling and sample coding

Epilithic diatom samples were obtained from each survey site on two occasions; April 1995 (spring sample) and July 1995 (summer sample). Stream samples were obtained by staff from the Catchment Research Group, University of Wales College of Cardiff, and lake samples obtained by staff from the Institute of Terrestrial Ecology, Bangor. Samples were coded in the field by date and NRA site code. These NRA site codes are incompatible with the Environmental Change Research Centre's (ECRC) AMPHORA database. Consequently in this report samples have been re-coded, and these ECRC codes are used throughout the report. Full site and sample details, with NRA and ECRC codes, are provided in appendix A.

Samples were taken according to the protocols of the Acid Waters Monitoring Network (see Patrick *et al.* 1991). At stream sites ten cobble sized stones were selected from pools at a depth below that of minimum flow. At lake sites ten cobble sized stones were selected from the permanently submerged littoral, with areas close to inflow or outflow streams being avoided. Epilithic diatoms were removed by brushing into a tray, decanting into plastic vials and were preserved with Lugols iodine.

2.2 Diatom sample preparation and enumeration

On arrival at the laboratory all diatom samples were logged and site and sample details added to the AMPHORA database. Samples were prepared for diatom analysis using the standard Environmental Change Research Centre procedures and Quality Assurance protocols (Battarbee 1986, ECRC 1996). Diatoms were examined and enumerated by light microscopy at x1000. Three hundred valves were counted from each sample and identified to species level, and the abundance of each taxon expressed as a percentage of the total count. Identification and nomenclature follows that developed by the Royal Society Surface Waters Acidification (SWAP) Programme (Flower & Kreiser 1988, Stevenson *et al.* 1991, Battarbee 1994). Consistent taxonomy was maintained between the diatom counts via the internal laboratory Analytical Quality Control (AQC) procedures detailed by Munro *et al.* (1990), including

exchange of slides and taxonomic harmonization for consistency with SWAP. Diatom solutions and slides are archived at the ECRC for inter-laboratory quality control. Additional sets of slides were prepared for archiving at the Natural History Museum and National Museum of Wales. The diatom data are stored in numerical format in the ECRC's AMPHORA database (Beare 1996 and see the ECRC's internet web page, <http://www.geog.ucl.ac.uk/~abeare/Amphora.html>).

Although the taxonomy used in this report follows SWAP (Stevenson *et al.* 1991), several undescribed taxa were identified which are not present in the SWAP database. These taxa have been assigned temporary species codes, and include *Achnanthes* [cf. *doenensis*], *Navicula* [cf. *subrotunda*], *Nitzschia* [cf. *palea*], *Achnanthes* [cf. *minima*] and *Achnanthes* [cf. *strenzkii*]. Additionally it was decided not to separate the taxa *Gomphonema angustatum* and *Gomphonema parvulum*. These taxa represent a complex of forms (see Krammer & Lange-Bertalot 1986), are difficult to separate in softwaters and have often been confused elsewhere (see Patrick *et al.* 1995). In this study they are combined into the taxon *Gomphonema* [*angustatum/parvulum*], a strategy consistent with the Acid Waters Monitoring Network (Patrick *et al.* 1995).

A total of 238 diatom samples were collected during the survey. Two stream sites (W071 and W072) were dry during the July 1995 sampling period and no diatom sample was obtained. Two of the remaining samples (W059A and W072A) were devoid of diatoms. Additionally, eight samples contained very low concentrations of diatoms, despite repeated preparation and concentration of sample material. In these cases it was not possible to identify 300 valves and a smaller count was obtained (W020A - 60 valves; W020B - 186 valves; W026B - 100 valves; W053A - 45 valves; W059B - 99 valves; W073A - 101 valves; W101A - 87 valves; W101B - 142 valves). Although total counts for these samples are low they have still been included in the data analyses. Problems with low concentrations in epilithic diatom samples are uncommon but can occur when sampling temporally dynamic streams. In high flow conditions care needs to be taken to sample diatoms above the level of minimum flow. It is possible that the problematic samples were taken from ephemerally flooded areas of the stream bed.

Diatom data is therefore available for 236 samples from 120 sites, and a total of 242 taxa were identified. The stream sample dataset contains 204 samples and 204 taxa, and the lake sample dataset contains 32 samples and 161 taxa. Full lists of taxa, taxon codes and authorities for the lake and stream samples are provided in appendices B and C.

2.3 Data analysis

2.3.1 Data manipulation

Diatom data were manipulated to calculate species abundance and occurrence using the program TRAN written by Steve Juggins. Sample diversity was calculated using Hill's N_2 (Hill 1973). This provides a relatively simple diversity measure corresponding to the *effective* number of species present in a sample (see Ludwig & Reynolds 1988).

A series of multivariate data analyses were performed on the two diatom dataset to (i) explore the main gradients of floristic variation, (ii) identify environmental variables accounting for a significant proportion of the variance in diatom data, and (iii) produce a classification of diatom samples. The diatom samples contained many rare taxa occurring in very low abundances. In proportional data of this type, rare taxa provide little ecological information and consequently prior to ordination and

classification the datasets were screened by excluding taxa occurring in less than five samples which also achieved a maximum relative abundance of less than 2%. The screened stream dataset contains 108 taxa, and the screened lake dataset 81 taxa. Stream sample W071A was excluded from multivariate analysis of the stream diatom data, as environmental data (chemistry and catchment variables) were unavailable for this site. The multivariate analyses of stream diatom data are therefore based on 203 samples.

Table 1 Environmental variables included in the data analyses

Water-chemistry variables:	Alkalinity (mg l ⁻¹ CaCO ₃) pH Hardness (mg l ⁻¹ CaCO ₃) H ⁺ (mg l ⁻¹) Conductivity (μS cm ⁻¹) Calcium (Ca ²⁺) (mg l ⁻¹) Magnesium (Mg ²⁺) (mg l ⁻¹) Sodium (Na ⁺) (mg l ⁻¹) Potassium (K ⁺) (mg l ⁻¹) Sulphate (SO ₄ ²⁻) (mg l ⁻¹) Total oxidised nitrogen (TON-N) (mg l ⁻¹) Total organic nitrogen (TORN-N) (mg l ⁻¹) Chloride (Cl ⁻) (mg l ⁻¹) Aluminium (Al) (mg l ⁻¹) Zinc (Zn) (μg l ⁻¹) Manganese (Mn) (μg l ⁻¹) Iron (Fe) (μg l ⁻¹) Dissolved organic carbon (DOC) (mg l ⁻¹)
Catchment variables:	Area (km ²) % conifer afforestation (%conifer) Average catchment gradient (Gradient) Site altitude (Alt) % Brown earth soils (%BrEarth) % Brown podzolic soils (%BrPodz) % Stagno-podzolic soils (%StagPod) % Gley soils (%Gley) % Peat soils (%Peat) Distance to west coast (ToWCoast)
River Habitat Survey variables:	Eight synthetic variables based on PCA analysis of Environment Agency River Habitat Surveys (RHS) of the stream sites PCA-spot (four axes) PCA-sweep (four axes)
Sampling period:	Spring samples (1/0) Summer samples (1/0)

Table 1 indicates the environmental variables available and included in the data analyses. Spot water

chemistry was used in the analyses, with water chemistry samples taken on 10/11 April 1995 used for the spring diatom samples (30 March - 27 April 1995) and water chemistry taken on 10/11 July 1995 used for the summer diatom samples (21 June - 21 July 1995). Spot water chemistry samples were used in preference to mean or seasonal data due to the rapid turnover rates of epilithic diatom communities with changing environmental conditions reported in the literature (e.g. Cox 1990a, 1990b, Moore 1977). However, exploratory analyses of the diatom data against mean annual chemistry revealed very similar overall results to the analyses based on the spot chemistry samples. Only the latter are presented in this report.

Prior to the multivariate analyses environmental variables were transformed as appropriate to normalize distributions. The following variables were transformed by $\log(x+1)$: %conifer, %BrEarth, % BrPodz, %StagPod, %Gley, %Peat, H, alkalinity, hardness, conductivity, Cl, SO₄, Na, K, Mg, Ca, Al, Zn, Mn, Fe, TON-N, TORN-N, DOC. The variables Area and ToWCoast were normalised by log transformation, and the River Habitat Survey PCA variables, pH, altitude and sampling period variables were not transformed as their distributions were approximately normal.

2.3.2 Ordination

Detrended correspondence analysis (DCA) (Hill & Gauch 1980) was used to identify the main patterns of floristic variation in the diatom data. DCA is an indirect gradient technique which assumes a unimodal response of species to their environment (ter Braak & Prentice 1988), and provides a robust ordination technique for data that have a large number of taxa and many zero values. DCA with detrending by polynomials was undertaken on the diatom data in the stream and lake sample datasets using CANOCO version 3.10 (ter Braak 1990a, 1990b). The DCA can be displayed as species and sample plots, in which the samples that lie close to the point of a species are likely to have a high abundance of that species and the probability of occurrence of a species declines with distance from its location on the plot.

The relationship between diatom data and environmental variables in both datasets was explored using canonical correspondence analysis (CCA) (ter Braak 1986, 1987). CCA is a multivariate direct gradient analysis technique, in which ordination axes are constrained to be linear combinations of environmental variables. CCA can therefore be used to identify the environmental variables which directly account for variance in the diatom data. CCA was implemented on the diatom data in the stream and lake datasets using CANOCO version 3.10 (ter Braak 1990a, 1990b). An additional feature of CANOCO 3.10 is the ability to identify the minimal number of explanatory environmental variables to be included in the ordination which explain a statistically significant proportion of the variance in diatom data. This is implemented through CANOCO's forward selection procedure, analogous to stepwise multiple regression (ter Braak 1990b), with Monte Carlo permutation tests (499 unrestricted permutations) to test the significance of the selected variables. In CCA of the lake and stream diatom datasets, forward selection was used to identify subsets of environmental variables that independently explained significant ($P \leq 0.05$) amounts of variation. Probability levels were adjusted for Bonferroni inequality (Manly 1991).

In the resulting CCA ordination diagrams, arrows represent environmental variables and point in the direction of maximum change. The length of the arrows represents the magnitude of change in that direction. Environmental variables with long arrows are more strongly correlated with the ordination axes, and are also more closely related to patterns of floristic variation, than variables with short arrows

(ter Braak 1986). Weighted intra-set correlation coefficients indicate the relative contribution of environmental variables in determining the axes derived from ordination of the species data.

Analysis of the stream diatom data also included a series of partial CCAs (ter Braak 1986) based on three types of explanatory variables; water chemistry, catchment variables and sampling period. The variance in the diatom data was partitioned into components representing (i) the unique contribution of the three types of environmental variable; (ii) the interaction or conditional effects between the variable types; and (iii) unexplained variance (Borcard *et al.* 1992). This approach allowed the relative influence and interactions of chemistry, catchment factors and sampling period on the diatom data to be evaluated (e.g. Jones & Juggins 1995, Qinghong & Bråkenhielm 1995).

Diatom species data were transformed by square root transformation prior to all ordination analyses in order to stabilize variance, and rare species were downweighted (ter Braak 1990a). Environmental variables were transformed as outlined above. Ordination diagrams were prepared using the program CALIBRATE (Juggins & ter Braak 1992).

2.3.3 Sample classification

Diatom samples from the stream and lake datasets were classified into sample groups by two-way indicator species analysis of the diatom percentage data using the program COINSPAN (Carleton *et al.* 1996a). COINSPAN is an extension of the commonly used classification technique TWINSPAN (Hill 1979). In a COINSPAN analysis the classification is constrained by a set of supplied environmental variables, and the resulting sample groups can be interpreted directly in terms of explanatory factors. A further advantage of the technique is that with noisy data (e.g. epilithic diatom data) COINSPAN can potentially provide a more stable and interpretable classification than produced by TWINSPAN analysis (see Carleton *et al.* 1996b). COINSPAN analysis was performed on the stream and lake datasets using the transformed environmental variables forward selected during canonical correspondence analysis.

3 Stream samples

3.1 Diatom occurrence and abundance

Figure 1 shows the relationship between diatom occurrence and maximum abundance in the stream samples. The majority of taxa plot in the lower left corner and occur in low abundance in relatively few samples. However, several taxa occur in a large number of the samples and can dominate the assemblages. These taxa include *Eunotia exigua*, *Achnanthes minutissima*, *Tabellaria flocculosa*, *Eunotia vanheurckii* var. *intermedia* and *Gomphonema [angustatum/parvulum]*. The dataset also includes taxa which can be abundant, but in relatively few samples (e.g. *Cocconeis placentula*, *Eunotia naegelii* and *Pinnularia irrorata*) and less abundant taxa which are nevertheless common (e.g. *Eunotia incisa*, *Synedra minuscula* and *Fragilaria vaucheriae*). The number and distribution of taxa within the samples can be summarised using a measure of sample diversity (see Juggins 1992). Table 2 indicates that the majority of samples have very low diversity, with c.77% of the samples having N_2 values < 4. Additionally 33% of the samples have N_2 values < 2 and can be considered species poor. These findings reflect Juggins (1992) study of diatoms in Scottish streams, and a general tendency for epilithon diatom samples in acid streams to be dominated by a very few abundant taxa.

Figure 1 Scatterplot of diatom occurrence and maximum abundance in the stream samples

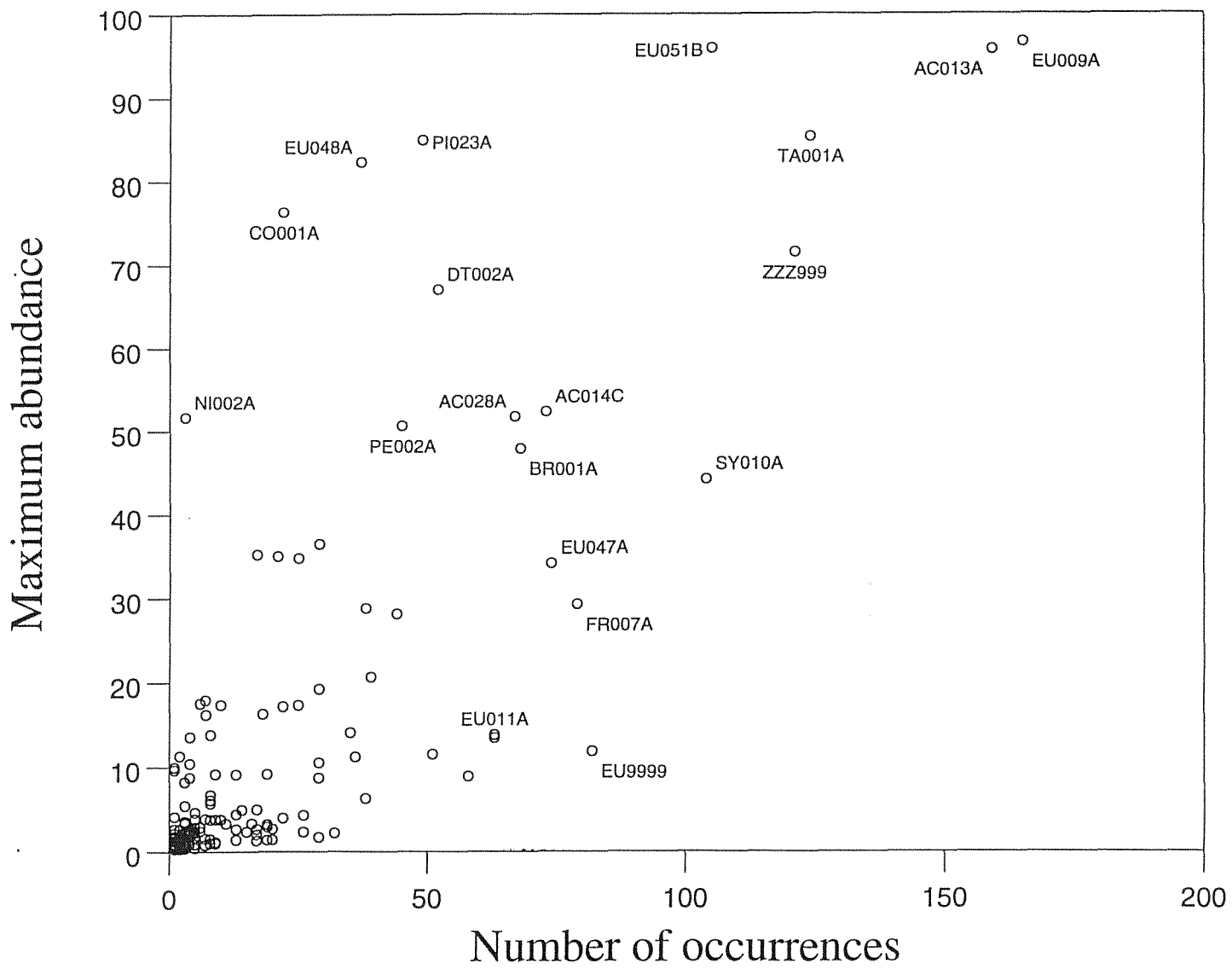


Table 2 Frequency distribution of N_2 sample diversity for stream samples

N_2 diversity	0-2	2-4	4-6	6-8	8-10	>10
No. of samples	68	88	30	9	5	3

3.2 Detrended correspondence analysis (DCA)

The main patterns of floristic variation in the stream diatom dataset were analysed using DCA. In the analysis detrending was by third order polynomials (ter Braak 1990b), species data were transformed by square root transformation, and rare species were downweighted (ter Braak 1990a).

The DCA axes do not capture a large proportion of the variance in the species data (Table 3), and the first two axes account for 20% of the cumulative variance in diatom data. This relatively low percentage of variance explained is typical of noisy data sets such as this, which contain a large number of samples, taxa and zero values (e.g. Stevenson *et al.* 1991). As DCA and CCA are data reduction techniques (Hill & Gauch 1980, ter Braak 1986), the amount of variance explained is not as important as the significance of the ordination axes and the ecological patterns revealed by the analyses (ter Braak 1988, Pienitz *et al.* 1995). DCA analyses effectively identify coherent ecological signals on the first few ordination axes, with noise in the data represented on latter axes (see Hill & Gauch 1980).

The DCA shows one dominant axis of variation ($\lambda_1 = 0.523$) which explains 13.2% of the variation in the floristic data (Table 3). This first DCA axis is strongly correlated with variables reflecting acid-base status, including alkalinity ($r = 0.718$), pH ($r = 0.676$), hardness ($r = 0.662$), calcium ($r = 0.656$) and aluminium ($r = -0.450$), and represents a gradient from samples with low pH/alkalinity (e.g. W003A, W028B, W029A) to samples with high pH/alkalinity (e.g. W051A, W046B, W086A) (Figure 2). Taxa with high axis 1 scores include *Achnanthes minutissima*, *Cocconeis placentula*, *Amphora pediculus* and *Achnanthes lanceolata*, all species known to occur in relatively high pH surface waters (Figure 3). Conversely, taxa with low axis 1 scores include acidophilous (i.e. pH preference < 7) to acidobiontic (i.e. pH preference < 5) taxa such as *Eunotia exigua*, *Eunotia rhomboidea*, *Peronia fibula* and *Navicula leptostriata*.

The second DCA axis explains a smaller fraction of the variance ($\lambda_2 = 0.256$), and represents a gradation within sites with low axis 1 scores. Sites with high axis 2 scores include W066A, W028B and W073A, and are associated with taxa such as *Tabellaria flocculosa*, *Eunotia denticulata*, *Eunotia naegelii* and *Brachysira brebissonii* (Figures 2 and 3). Sites with low scores on this axis are associated with taxa such as *Achnanthes austriaca* var. *helvetica* and *Eunotia vanheurckii* var. *intermedia*, and include W110A, W013A and W091A. The axis is correlated with a variety of environmental variables (see Table 3), most notably %Conifer ($r = -0.430$), Fe ($r = 0.319$) and Gradient ($r = 0.318$).

Later axes are less important in explaining variance in the diatom data ($\lambda_3 = 0.182$, $\lambda_4 = 0.139$). DCA axis 3 accounts for 4.6% of the variance, and is most strongly correlated with gradient ($r = 0.300$) and Fe ($r = -0.308$). *Peronia fibula* has a high score on DCA axis 3, and *Pinnularia irrorata*

Figure 2 DCA sample plot for stream samples

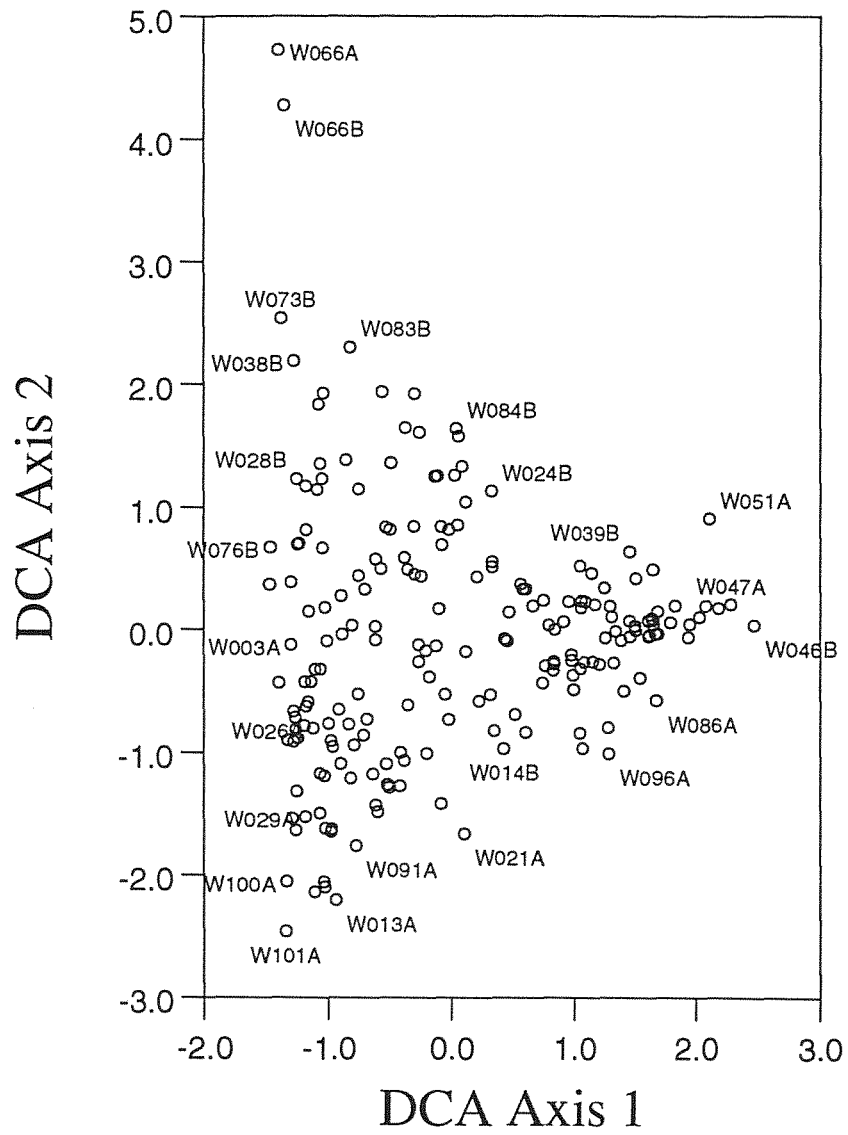
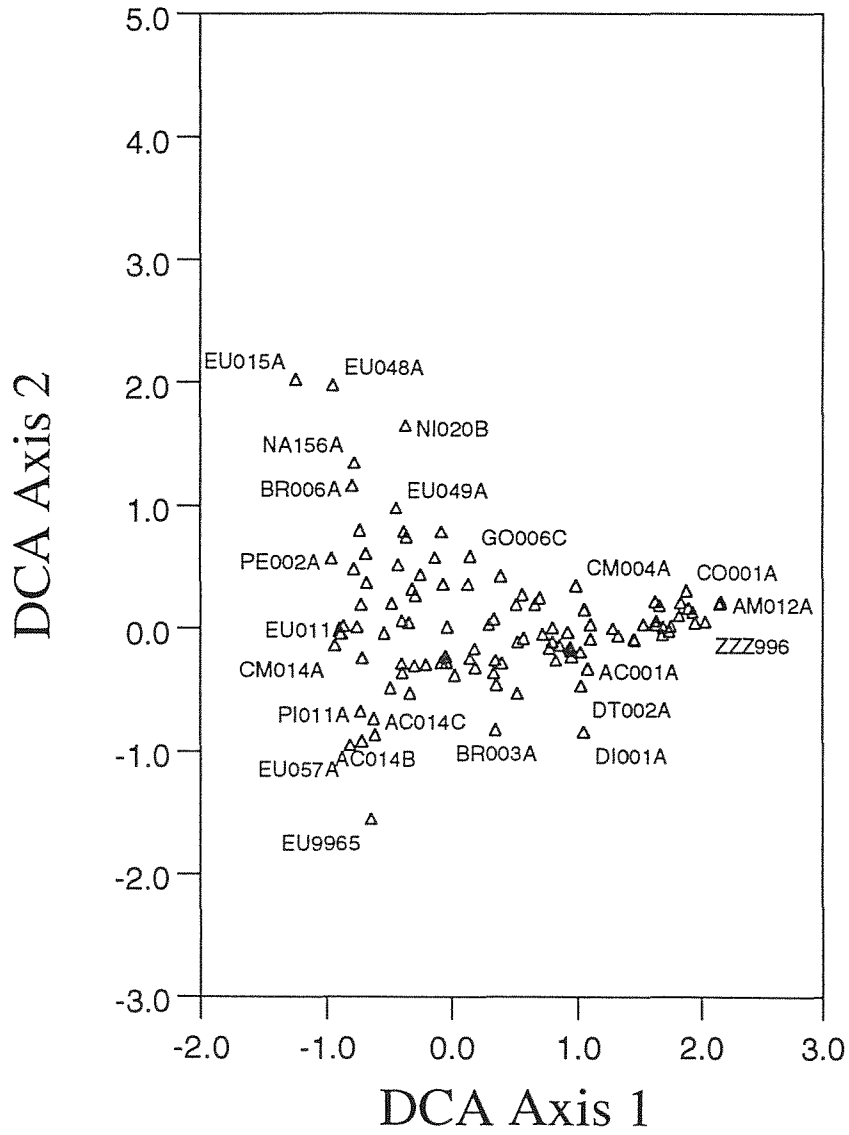


Figure 3 DCA species plot for stream samples



a low score on this axis. The fourth axis accounts for 3.5% of the variance; taxa with high scores include *Amphora pediculus* and *Gomphonema intricatum*, and taxa with low scores include *Hannea arcus* and *Diatoma hyemale*. The axis is correlated with TON-N ($r = 0.173$), Mg ($r = 0.165$) and %Conifer ($r = 0.159$) (Table 3).

Table 3 DCA results for the 203 stream samples, where r is the correlation between environmental variables and the ordination axis. Only statistically significant values ($p \leq 0.05$) are shown for selected environmental variables

	DCA axis 1	DCA axis 2	DCA axis 3	DCA axis 4
Eigenvalue	0.523	0.256	0.182	0.139
Variance explained	13.2 %	6.4 %	4.6 %	3.5 %
pH	$r=0.676$	-	-	-
Alkalinity	$r=0.719$	$r=0.155$	-	-
Conductivity	$r=0.607$	-	-	-
Hardness	$r=0.662$	-	-	-
Ca	$r=0.656$	-	$r=0.153$	-
Mg	$r=0.560$	-	-	$r=0.165$
Na	$r=0.194$	$r=-0.267$	-	-
Al	$r=-0.450$	$r=-0.220$	-	-
Mn	$r=-0.597$	-	$r=-0.137$	-
Fe	$r=-0.345$	$r=0.319$	$r=-0.308$	-
TON-N	$r=0.433$	$r=-0.259$	$r=0.243$	$r=0.173$
%Conifer	$r=-0.159$	$r=-0.430$	-	$r=0.159$
Gradient	-	$r=-0.318$	$r=0.300$	-
Altitude	$r=-0.189$	$r=0.233$	$r=-0.231$	$r=-0.159$
%BrEarth	$r=0.414$	-	-	-
%BrPodz	-	$r=-0.259$	$r=0.212$	-
%StagPod	-	$r=-0.138$	-	-
Spring/Summer	-	$r=0.241$	-	-

3.3 Canonical correspondence analysis (CCA)

CCA was used to directly explore the relationships between the stream diatom assemblages and environmental variables. The results of forward selection of environmental variables for CCA are shown in Table 4. The analysis identified a minimal subset of 13 environmental variables that independently explained significant ($P \leq 0.05$) proportions of the variance in the diatom species data. Alkalinity and Fe represent 47% of the total variance explained by the 13 environmental subset, indicating their importance as explanatory variables. Although the first environmental variable selected in the procedure was alkalinity, Table 4 indicates that prior to forward selection several other variables indicative of acid-base status (e.g. pH, hardness, calcium) could also account for relatively large fractions of the variance. Due to the strong co-variance with alkalinity these variables were not subsequently also selected in the

procedure.

Table 4 Variance potentially explained by selected environmental variables before forward selection, and variance explained with the addition of each environmental variable during forward selection in CCA of stream sample data.

Variable	Before forward selection	Added with selection
Alkalinity	0.30	0.30
Fe	0.17	0.15
Mn	0.22	0.06
Mg	0.21	0.06
%BrEarth	0.16	0.06
%StagPod	0.05	0.05
%Conifer	0.08	0.05
Na	0.07	0.05
Spring/Summer	0.05	0.04
%BrPodz	0.06	0.04
Gradient	0.09	0.04
Altitude	0.08	0.04
TON-N	0.16	0.03
Calcium	0.28	
Hardness	0.28	
pH	0.26	
Conductivity	0.25	
Aluminium	0.13	
DOC	0.10	
	Sum of variance	0.96

CCA was performed on the stream diatom dataset using the 13 forward selected environmental variables. The CCA (Table 5) shows one dominant axis of variation ($\lambda_1 = 0.386$) explaining 9.7% of the variance in the diatom data, and a second, smaller axis ($\lambda_2 = 0.173$) explaining a further 4.4% of the floristic variation. These axes are both significant on the basis of Monte Carlo permutation tests ($P < 0.01$; 499 permutations). CCA axis 1 shows a strong correlation with alkalinity ($r = 0.751$), Mg ($r = 0.609$) and Mn ($r = -0.620$), and separates low alkalinity samples with high levels of Mn from higher alkalinity samples with high levels of Mg and TON-N and relatively high proportions of brown earth soils in the catchment. Samples with high axis 1 scores include W065B, W048B and W046A (Figure 4), and are associated with circumneutral taxa such as *Cymbella laevis*, *Amphora pediculus*, *Achnanthes minutissima*, *Fragilaria vaucheriae* and *Cocconeis placentula* (Figure 5). Samples with low axis 1 scores include W026B, W035B and W017B, and are associated with acidophilous to

Figure 4 CCA sample-environmental variable biplot for stream samples

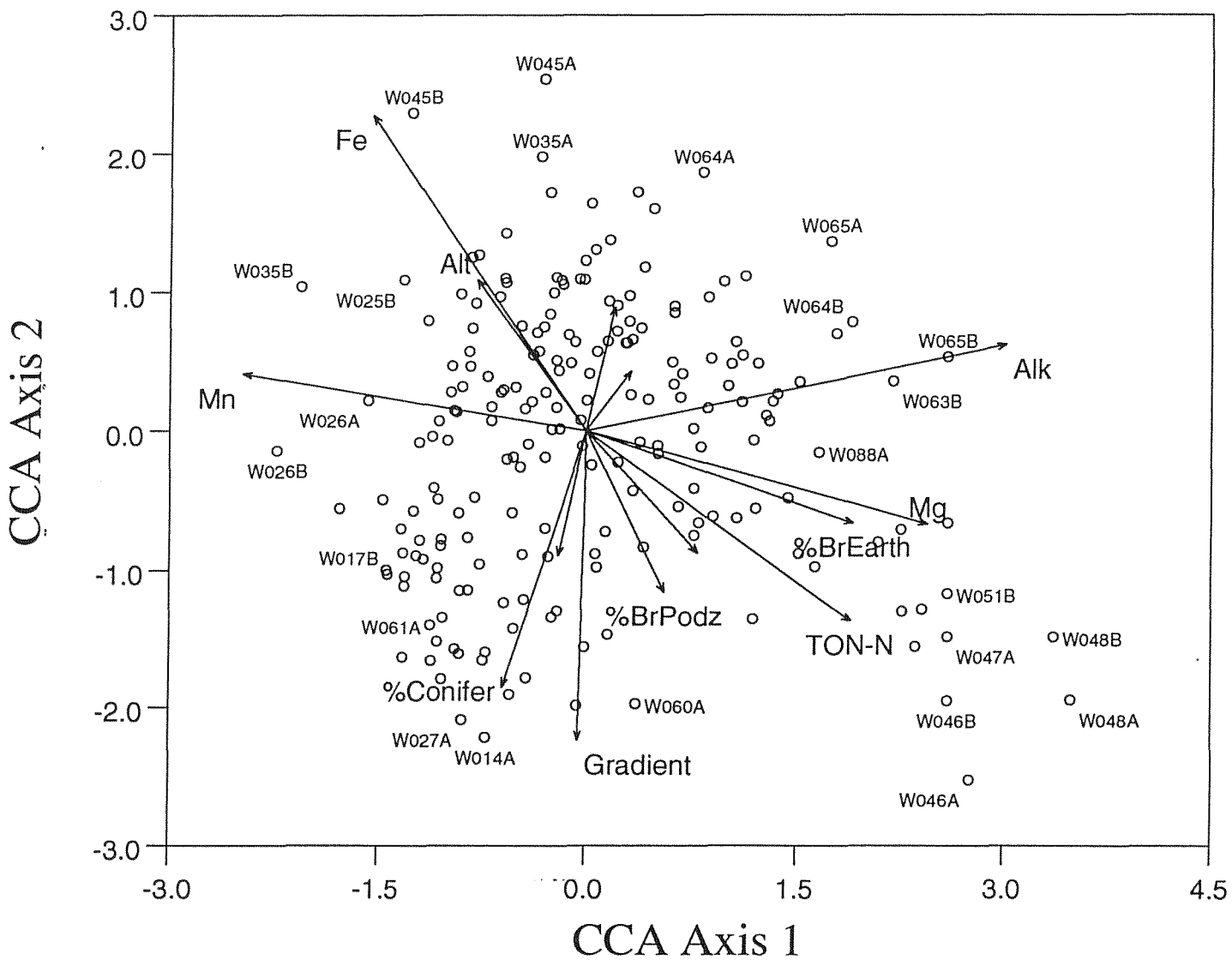
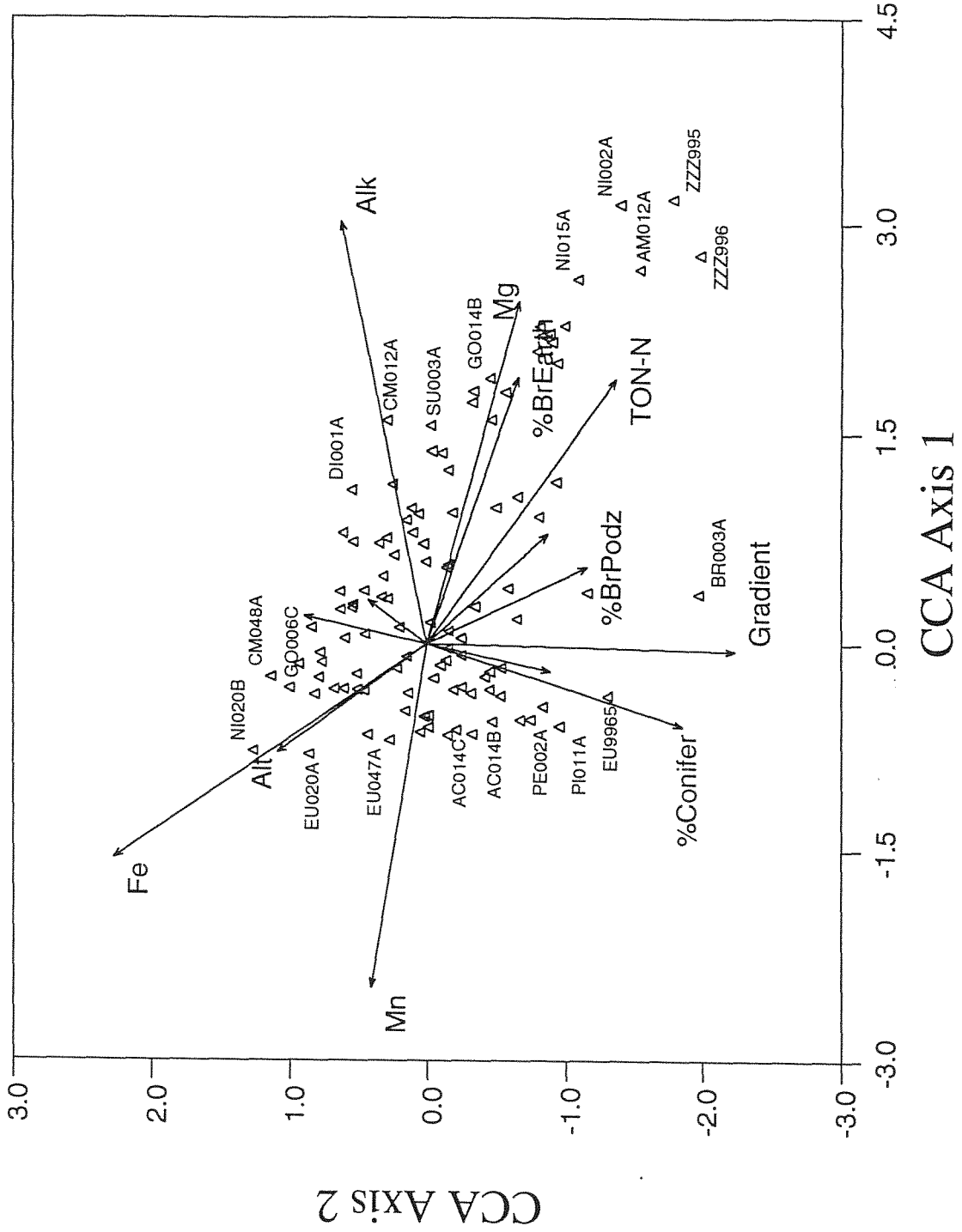


Figure 5 CCA species-environment variable biplot from stream samples



acidobiontic taxa such as *Eunotia incisa*, *Eunotia exigua*, *Achnanthes austriaca* var. *helvetica* and *Peronia fibula*. The second axis is most strongly correlated with Fe ($r = 0.528$), gradient ($r = -0.518$) and %conifer ($r = -0.430$). Samples with low axis 2 scores (e.g. W060A and W014A) are associated with catchments with large gradients and % conifer cover, with taxa such as *Brachysira seriants*, *Eunotia vanheurckii* var. *intermedia* and *Eunotia* [sp.10 (*minima*)] common. Samples with high axis 1 scores are associated with high concentrations of Fe in stream waters, and with taxa such as *Cymbella lunata* and *Eunotia meisteri*.

Although later axes in the CCA are less important ($\lambda_3 = 0.107$, $\lambda_4 = 0.06$), they are still statistically significant on the basis of Monte Carlo permutation tests ($P < 0.01$; 499 permutations). The third axis is most strongly correlated with altitude ($r = 0.383$), %BrEarth ($r = 0.351$) and %StagPod ($r = -0.327$), and the fourth axis is most strongly correlated with %StagPod ($r = -0.341$).

Table 5 CCA results for the 203 stream samples, where r is the correlation between environmental variables and the ordination axis. Only statistically significant values ($p \leq 0.05$) are shown for the forward selected environmental variables

	CCA axis 1	CCA axis 2	CCA axis 3	CCA axis 4
Eigenvalue	0.386	0.173	0.107	0.060
Variance explained	9.7 %	4.4 %	2.7 %	1.5 %
Alkalinity	$r=0.751$	$r=0.143$	$r=0.191$	-
Mg	$r=0.609$	$r=-0.155$	$r=0.165$	-
Na	$r=0.198$	$r=-0.203$	$r=-0.208$	-
Mn	$r=-0.602$	-	$r=0.217$	-
Fe	$r=-0.387$	$r=0.528$	$r=0.252$	-
TON-N	$r=0.470$	$r=-0.318$	-	-
%Conifer	$r=-0.148$	$r=-0.430$	-	$r=-0.257$
Gradient	-	$r=-0.518$	-	-
Altitude	$r=-0.196$	$r=0.252$	$r=0.383$	-
%BrEarth	$r=0.474$	$r=-0.153$	$r=0.351$	-
%BrPodz	$r=0.139$	$r=-0.269$	$r=-0.152$	-
%StagPod	-	-	$r=-0.327$	$r=-0.341$
Spring/Summer	-	$r=0.207$	-	$r=0.164$

3.4 Variance partitioning

Table 6 summarizes the results of the partial CCAs, and indicates how the variance in diatom data in the stream sample dataset is partitioned into components representing the unique contribution of different variable types and interactions between variable types. The results emphasise the importance of chemistry in explaining variation in the diatom data. Chemistry makes an independent contribution of 10.4%, and there is also a large interactive component (5.9%) between the chemistry and catchment

variables, reflecting co-variance between important chemical and catchment variables. The catchment variables alone (i.e. independent of chemistry) also explain a significant fraction (6.7%) of the variance in diatom data. The only other significant contribution is by sampling period alone, which is significant despite explaining a relatively small amount of the total variance (1.1%).

The large fraction of unexplained variation is typical for ecological analyses of this type, and is comparable to the findings of other multivariate analyses of diatom-environment relationships (e.g. Stevenson *et al.* 1991, Pienitz *et al.* 1995) and invertebrate-environment relationships (e.g. Gower *et al.* 1994). The model fit is for the square root percentage data for each of the 204 diatom taxa in each of the 203 samples, and is therefore a rather strict test of the relationships with the environmental variables. As the data include many rare taxa occurring in low abundances it is inherently noisy, and this noise will be partly responsible for the unexplained variation. However, the Monte Carlo permutation tests indicate that the unexplained variation is significant, and therefore that there is systematic variation in the diatom assemblages not explained by the measured environmental variables. This variation may be due to aspects of streamwater flow not well represented in the dataset (e.g. episodicity of storm events) or to other environmental factors important to diatom assemblages such as light and temperature conditions.

Table 6 Results of partitioning the variance in the stream diatom data. Significance values were determined by Monte Carlo permutation tests ($P \leq 0.05$; 499 permutations)

Chemical variables:	Alkalinity, Fe, Mn, Mg, Na, TON-N
Catchment variables:	%BrEarth, %StagPod, %Conifer, %BrPodz, Gradient, Alt
Sampling period variable:	Spring/Summer

Source of variation	Percentage	Significance
Unexplained variation	75.80	0.01
Explained by chemistry independent of other variables	10.43	0.01
Explained by catchment variables independent of other variables	6.69	0.01
Explained by sampling period independent of other variables	1.06	0.01
Explained by co-variance between chemistry and catchment variables	5.86	0.01
Explained by co-variance between chemistry and sampling period variables	0.15	ns
Explained by co-variance between catchment and sampling period variables	0.00	ns
Explained by co-variance between chemistry, catchment and sampling period variables	0.00	ns

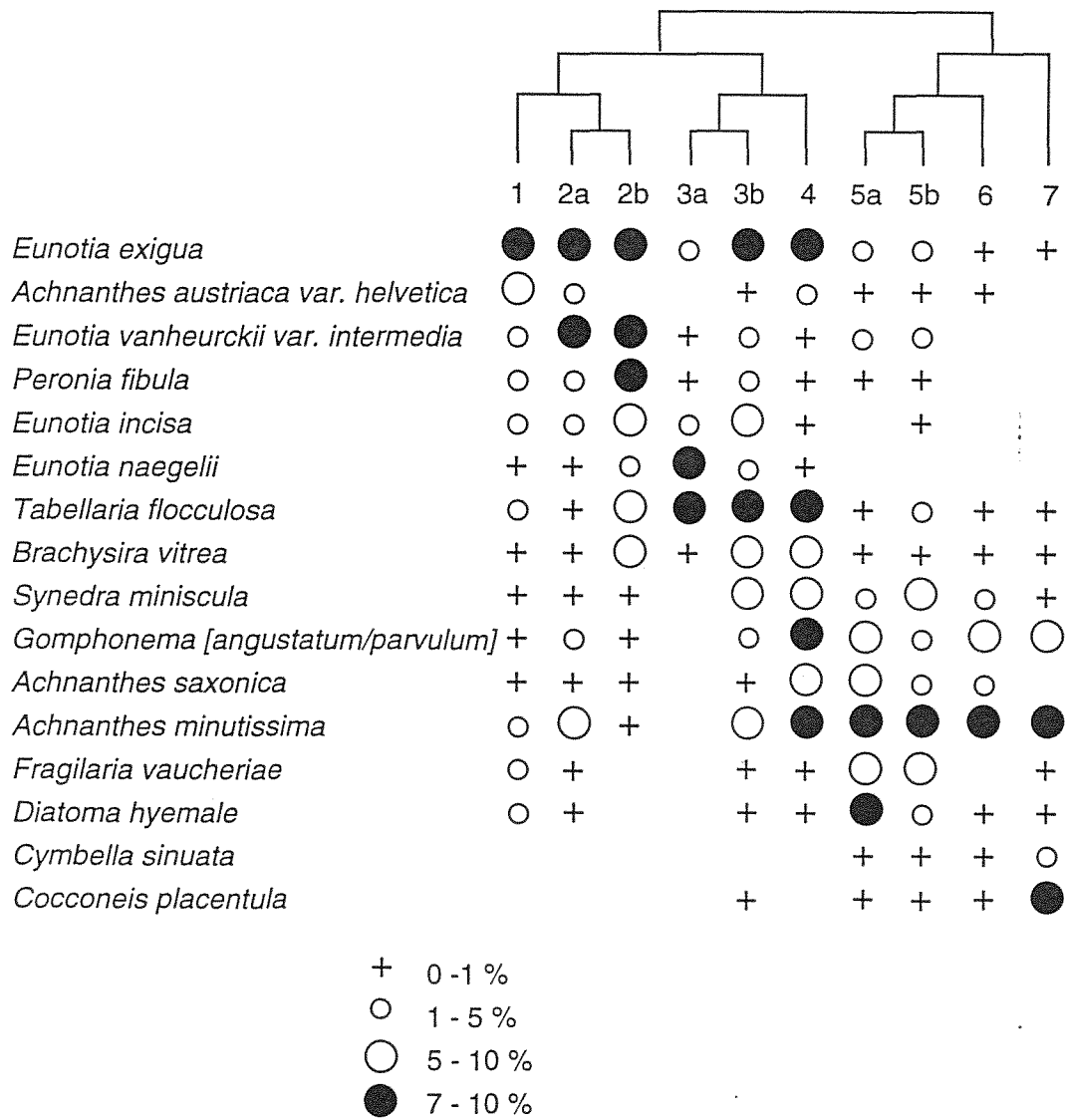
3.5 COINSPAN sample classification

The COINSPAN classification for the stream samples is shown in Figure 6, which indicates the mean abundance of common taxa in each group. Seven groups of samples were defined at three levels of division, and 10 subgroups defined at four levels of division. The first division, strongly associated with alkalinity, recognises the acidophilous/acidobiontic *Eunotia exigua*, *E. incisa* and *E. rhomboidea* as negative indicators (i.e. preferential species for Groups 1-4) and the circumneutral *Achnanthes minutissima*, *Fragilaria vaucheriae* and *Cymbella minuta* as positive indicators (i.e. preferential to Groups 5-7). The second division includes *Eunotia vanheurckii* as a negative indicator and *Tabellaria flocculosa*, *Gomphonema [angustatum/parvulum]* and *Synedra miniscula* as positive indicators, and separates Groups 1 and 2 from Groups 3 and 4. The division is associated with a gradient of Fe, with samples in Groups 1 and 2 having higher Fe concentrations. The third dichotomy divides Groups 5 and 6 from Group 7, with *Cocconeis placentula*, *Amphora pediculus* and *Cymbella sinuata* being positive

Table 7 Mean values of forward selected environmental variables in the stream sample COINSPAN groups. Figure in parentheses represent standard deviations.

COINSPAN group	1	2a	2b	3a	3b	4	5a	5b	6	7
no. of samples	40	27	12	2	12	35	15	34	16	10
Alkalinity	1.83 (3.54)	2.74 (4.09)	4.50 (8.65)	0 (-)	5.25 (6.41)	5.22 (3.48)	4.67 (2.69)	12.26 (17.76)	32.07 (23.67)	69.7 (18.2)
Na	5.04 (0.94)	5.87 (1.31)	4.75 (1.36)	4.40 (-)	5.07 (1.70)	4.43 (0.63)	5.66 (0.91)	5.41 (1.10)	5.71 (1.49)	4.99 (0.75)
Mg	1.05 (0.38)	1.37 (0.48)	1.26 (0.78)	0.72 (-)	1.27 (0.77)	1.15 (0.39)	1.39 (0.37)	1.62 (0.62)	2.27 (0.76)	3.96 (2.11)
Mn	68.4 (47.8)	31.5 (23.7)	21.0 (22.1)	35.9 (-)	178.5 (217)	53.6 (111)	6.33 (8.5)	13.33 (19.9)	4.55 (3.71)	1 (-)
Fe	133 (163)	27 (29)	89 (163)	36 (-)	1167 (1737)	384 (576)	20 (34)	89 (113)	31 (63)	6 (7)
TON-N	0.14 (0.11)	0.40 (0.27)	0.19 (0.15)	0.05 (-)	0.06 (0.04)	0.10 (0.12)	0.29 (0.27)	0.39 (0.30)	0.56 (0.45)	0.61 (0.42)
%Conifer	38.4 (31.4)	60.2 (25.8)	26.4 (28.2)	0 (-)	1.7 (3.8)	8.9 (15.1)	16.9 (28.5)	28.0 (29.2)	9.5 (17.9)	27.1 (38.6)
Gradient	9.7 (3.1)	12.6 (3.7)	12.3 (5.7)	6.5 (-)	7.0 (4.7)	8.8 (2.2)	9.5 (4.7)	9.7 (3.5)	9.7 (3.7)	11.6 (3.7)
Altitude	281 (89)	192 (57)	266 (82)	190 (-)	332 (86)	276 (58)	200 (61)	208 (61)	256 (62)	258 (76)
%BrEarth	0 (0)	0.17 (0.87)	0 (0)	0 (-)	0 (0)	0.16 (0.58)	0.65 (1.73)	0.22 (0.62)	4.92 (10.3)	22.35 (21.7)
%BrPodz	7.4 (11.3)	35.9 (22.4)	15.3 (21.8)	0 (-)	7.4 (11.0)	14.0 (14.2)	23.9 (18.8)	18.8 (21.3)	17.2 (28.2)	39.2 (39.8)
%StagPodz	51.5 (30.4)	39.1 (26.8)	30.2 (36.5)	77.5 (-)	29.7 (22.7)	46.3 (27.0)	62.9 (18.8)	35.9 (17.7)	44.9 (28.3)	24.7 (22.3)
Spring sample	0.58	0.57	0.58	0.5	0.08	0.54	0.66	0.26	0.44	0.60
Summer sample	0.42	0.43	0.52	0.5	0.92	0.51	0.33	0.74	0.56	0.40

Figure 6 COINSPAN classification of stream samples, showing mean abundance of common taxa in each group



preferentials (group 7), and *Achnanthes minutissima*, *Fragilaria vaucheriae* and *Synedra miniscula* associated with the negative side of the division (Groups 5 and 6).

At the third level, division 4 has *Eunotia vanheurckii* var. *intermedia* and *Peronia fibula* as positive indicators (Group 2). This division is associated with catchment gradient, with samples in Group 2 having higher catchment gradients than samples in Group 1. Group 2 is further subdivided into subgroups 2a and 2b by the positive indicators *Peronia fibula* and *Tabellaria flocculosa* (preferential to subgroup 2b). Division 5 separates Groups 3 and 4, with *Eunotia incisa* and *Peronia fibula* as negative preferentials (Group 3) and *Achnanthes saxonica* and *Achnanthes minutissima* as positive preferentials (Group 4). At a lower level Group 3 is divided by the negative preferential *Eunotia naegelii* (preferential to subgroup 3a).

Division 6 divides Groups 5 and 6 on the basis of the negative preferentials *Eunotia exigua*, *Achnanthes saxonica*, *Diatoma hyemale* and *Eunotia vanheurckii* var. *intermedia* (Group 5). Group 5 is further divided by the indicator taxa *Achnanthes saxonica* and *Diatoma hyemale* (preferential to subgroup 5a) and *Tabellaria flocculosa* (preferential to subgroup 5b).

Table 7 shows mean values of the forward selected environmental variables in the COINSPAN groups, and Figure 7 presents a boxplot of COINSPAN groups against N₂ sample diversity.

The stream sample COINSPAN groups can be summarised according to their species composition and environmental characteristics.

COINSPAN Group 1 *Eunotia exigua/Achnanthes austriaca* var. *helvetica*

Low diversity samples dominated (> 50% abundance) by *Eunotia exigua*, but characterised by high abundances of *Achnanthes austriaca* var. *helvetica*. Other taxa occurring in the samples include *Eunotia vanheurckii* var. *intermedia*, *Tabellaria flocculosa* and *Eunotia incisa*. These species are indicative of acidophilous to acidobiontic conditions. The samples are associated with very low alkalinity, elevated levels of Mn and Fe and relatively high catchment altitudes (Table 7).

COINSPAN Group 2a *Eunotia vanheurckii* var. *intermedia/Eunotia exigua*

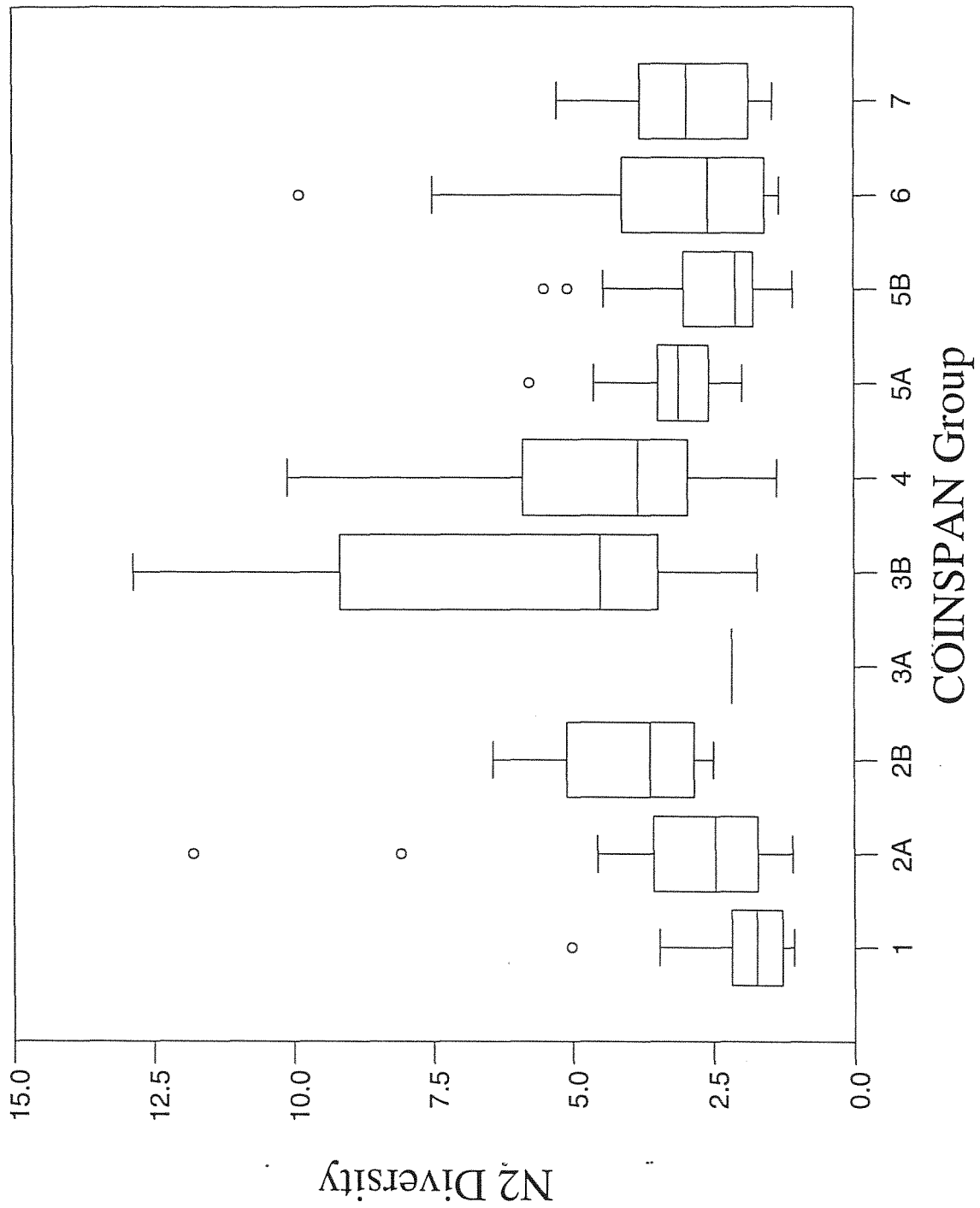
The samples in this subgroup are dominated by *Eunotia vanheurckii* var. *intermedia* (abundance generally > 40%) with *Eunotia exigua* also abundant. *Achnanthes minutissima* is present in many of the samples. The samples are associated with low alkalinity, high TON-N streams in catchments with large gradients and % conifer cover.

COINSPAN Group 2b *Eunotia exigua/Peronia fibula*

Characterised by co-dominance of *Eunotia exigua* and *Peronia fibula*. *Eunotia vanheurckii* var. *intermedia*, *Tabellaria flocculosa* and *Eunotia incisa* are also common in many of the samples. The species present in the samples are all acidophilous to acidobiontic. The samples are associated with relatively low, but variable alkalinity and high catchment gradients.

Figure 7

Boxplot of distribution of N_2 sample diversity across the stream sample COINSPAN groups



COINSPAN Group 3a *Eunotia naegelii/Tabellaria flocculosa*

This subgroup, containing only two samples, is characterised by the dominance (> 50%) of *Eunotia naegelii*, a species achieving only low abundance (< 5%) in other samples. The two samples in the subgroup both come from the same site (W066), which has very low measured alkalinity.

COINSPAN Group 3b *Eunotia exigua/Tabellaria flocculosa*

Characterised by co-dominance of *Eunotia exigua* and *Tabellaria flocculosa*. Several other taxa can also occur in high abundances, including *Brachysira vitrea*, *Eunotia incisa* and *Synedra miniscula*. The samples have relatively high diversity, and come from high altitude, low gradient streams with intermediate alkalinity levels. Some of the samples have exceptionally high levels of stream-water Fe and Mn. The majority of the samples (92%) were taken during the summer sampling period.

COINSPAN Group 4 *Eunotia exigua/Tabellaria flocculosa/Gomphonema [angustatum/parvulum]/Achnanthes minutissima*

These samples have high N₂ diversity, and are characterised by assemblages including *Eunotia exigua*, *Tabellaria flocculosa*, *Gomphonema [angustatum/parvulum]* and *Achnanthes minutissima*. Other taxa common in the samples include *Synedra miniscula*, *Brachysira vitrea* and *Achnanthes saxonica*. These species range between acidobiontic/acidophilous forms to more circumneutral taxa. The samples are associated with intermediate alkalinity, elevated (but variable) Mn and Fe, and relatively low catchment gradients.

COINSPAN Group 5a *Achnanthes minutissima/Diatoma hyemale*

Generally dominated by *Achnanthes minutissima*, but characterised by high abundances of *Diatoma hyemale*. *Fragilaria vaucheriae*, *Gomphonema [angustatum/parvulum]* and *Achnanthes saxonica* are also common. The taxa present in these samples are generally indicative of circumneutral conditions. The samples are associated with intermediate alkalinity, high TON-N, low altitude sites with catchment soils dominated by Stagno-podzols. The majority of the samples (66%) were taken during the spring sampling period.

COINSPAN Group 5b *Achnanthes minutissima*

The samples are characterised by low diversity and the dominance (>50%) of *Achnanthes minutissima*, with the occasional presence of more acidophilous taxa. *Synedra miniscula* and *Gomphonema [angustatum/parvulum]* are also usually present but in relatively low abundance. Other taxa occasionally present include *Fragilaria vaucheriae* and *Achnanthes saxonica*, with *Eunotia exigua* and *Tabellaria flocculosa* occurring in very low abundances. The samples have low N₂ diversity, and are associated with high stream-water alkalinity. The majority of the samples (74%) were taken during the summer sampling period.

COINSPAN Group 6 *Achnanthes minutissima/Gomphonema angustatum/parvulum]*

These samples are dominated by *Achnanthes minutissima*, with *Gomphonema [angustatum/parvulum]* common. *Cymbella minuta* and *Fragilaria vaucheriae* occur in low abundance in many of the samples. The samples are associated with very high stream-water alkalinity and TON-N.

COINSPAN Group 7 *Achnanthes minutissima/Cocconeis placentula*

Dominated by *Achnanthes minutissima* and characterised by the presence of *Cocconeis placentula*. Other species indicative of high alkalinity surface waters are also present, including *Amphora pediculus*

and *Cymbella sinuata*. The samples are associated with extremely high alkalinity values, high stream-water TON-N, and catchments with brown earth soils.

3.6 Discussion

The stream samples in general have low species diversity, and many are dominated by a few abundant taxa. This is an established characteristic of epilithic diatom samples from low pH/alkalinity upland streams (e.g. Juggins 1992, Round 1993). In the current dataset some of the samples are dominated by a single taxon (e.g. N_2 diversity < 2) and can be considered species poor. In particular, the samples in COINSPAN Group 1 are dominated by *Eunotia exigua*, and samples in COINSPAN Group 5b by *Achnanthes minutissima*. These two taxa are common across the entire sample dataset (see Figure 6), and their importance in stream diatom assemblages is apparent from many other studies (e.g. Leclercq 1977, Round 1991, Allott & Juggins 1991, Juggins 1992). In general, *Eunotia exigua* is associated with acidic streams (pH < 5.5), whereas *Achnanthes minutissima* is characteristic of more circumneutral conditions. The only other taxon which completely dominates samples in the dataset are *Eunotia naegelii* (which dominates the two samples in COINSPAN Group 3a), and *Pinnularia irrorata*. This latter taxon dominates sample W071A, which was taken from an ephemeral forest ditch and was excluded from the main data analyses. *Pinnularia irrorata* is often associated with ephemeral, highly acidic surface waters such as moorland pools. Several other taxa are common, but not dominant across the dataset. These include the acidophilous *Eunotia vanheurckii* var. *intermedia*, *Peronia fibula*, and *Tabellaria flocculosa*, the acidophilous-circumneutral *Brachysira vitrea*, and the circumneutral *Synedra miniscula*, *Gomphonema [angustatum/parvulum]* and *Fragilaria vaucheriae*.

The common taxa within the present dataset have also commonly been recorded in other studies of epilithic diatoms in Wales (e.g. Allott & Juggins 1991, Round 1991). Round (1993) has developed a general classification scheme for epilithic diatoms in British rivers, including those in Wales. The assemblages in the current study generally correspond to Round's Zone 1 assemblages, characteristic of low pH waters in the uppermost reaches of rivers and dominated by *Eunotia exigua* and *Achnanthes minutissima*. However, the samples in COINSPAN Group 7, characterised by the dominance of *Achnanthes minutissima* but with *Cocconeis placentula*, *Amphora pediculus* and *Cymbella sinuata* common, correspond to Round's Zone 3 which is indicative of nutrient rich waters with higher alkalinity (5-25 mg l⁻¹ CaCO₃). Allott and Juggins (1991) studied epilithic diatoms in 30 Welsh lakes and streams. Higher pH (6 - 6.5) stream sites were dominated by *Achnanthes minutissima*, with *Synedra miniscula* also common. Streams with pH within the range 5 - 6 were characterised by *Tabellaria flocculosa* and *Peronia fibula*. Round (1991) has also studied the epilithic diatom assemblages of streams flowing into Llyn Brianne, and identified four associations of diatoms. The first, characterised by *Eunotia exigua* and *Achnanthes marginulata* is not represented in the current study. The second of Round's (1991) associations, *Achnanthes minutissima/Cymbella minuta/Diatoma mesodon*, is reflected in some of the samples within COINSPAN group 5a. Round's third association contains *Eunotia vanheurckii* (possibly synonymous with *Eunotia vanheurckii* var. *intermedia* in this study) and *Eunotia exigua*, and matches the samples in COINSPAN Group 2a. The final association is characterised by *Eunotia exigua* with *Tabellaria flocculosa* and *Eunotia rhomboidea* also common, a combination of taxa found in some of the samples within COINSPAN Group 3a. The current study contains many more samples than have previously been studied from upland Welsh streams, and unsurprisingly contains a greater variety of assemblage types as reflected in the COINSPAN groups.

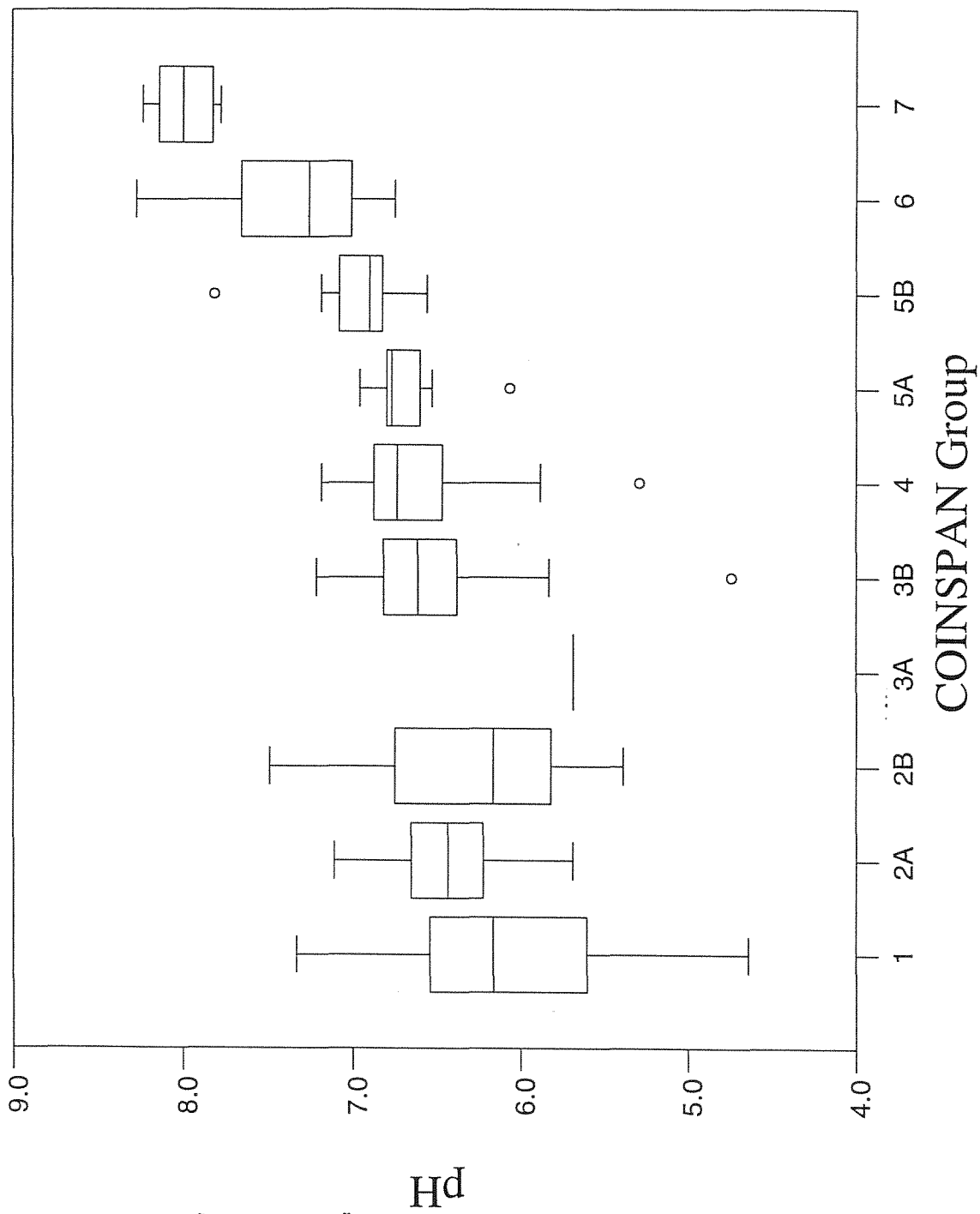
Some of the assemblages identified in the present study also correspond to those found in the 11 streams included in the Acid Waters Monitoring Network (AWMN) (Patrick *et al.* 1991, Patrick *et al.* 1995). All of the AWMN stream diatom assemblages contain taxa also apparent in the current dataset, and some of the assemblages correspond closely to the COINSPAN Groups defined in this study. For example, three of the AWMN sites (Old Lodge, Afon Hafren, Afon Gwy) are dominated by *Eunotia exigua* and have assemblages corresponding to COINSPAN Group 1. The AWMN sites at the Allt a'Mharcaidh, Allt na Coire nan Con and Coneyglen Burn are characterised by *Achnanthes minutissima*/*Synedra minuscula*/*Gomphonema [angustatum/parvulum]* and correspond to COINSPAN Group 5b. Beagh's Burn and the River Etherow are characterised by co-dominance of *Eunotia exigua* and *Achnanthes minutissima*, assemblages which are similar but less diverse than those in COINSPAN Group 4. However, some of the more acidic AWMN stream sites (pH < 5.5) contain assemblages of acidophilous taxa which are not well represented in the current dataset. These include the Dargall Lane (characterised by a combination of *Peronia fibula*, *Eunotia incisa* and *Eunotia naegelii*), and the Bencrom River (*Eunotia naegelii*/*Brachysira brebissonii*). The closest assemblages to these sites are provided by the two samples in COINSPAN Group 3a, which are dominated by *Eunotia naegelii*. The low pH (<5.5) sites in the current dataset tend to be dominated by *Eunotia exigua*. This contrasts with the low pH AWMN sites, where a greater variety of assemblage types represented.

The dominant gradient in diatom assemblages within the current dataset, as revealed by the first DCA axis, is very strongly associated with stream-water alkalinity and co-variables. This interpretation is reinforced by the CCA and COINSPAN analyses. The first CCA axis shows very similar patterns of species and sample variation as shown in the primary DCA axis, both being strongly correlated with alkalinity and co-variables of acid-base status. The COINSPAN groups also show a clear relationship with alkalinity (see Table 7). In the forward selection procedure alkalinity was the first variable selected, showing the strongest fit to the diatom data (Table 4). However, in the dataset pH is strongly correlated with alkalinity and consequently also shows a very strong relationship with the primary gradient in the diatom data. This is emphasised by the strong relationship between pH and the stream sample COINSPAN groups (Figure 8).

Common species associated with very low stream-water alkalinity (< 4.5 mg l⁻¹) and pH (< 6.5) include *Eunotia exigua*, *Achnanthes austriaca* var. *helvetica*, *Eunotia vanheurckii* var. *intermedia*, *Peronia fibula* and *Eunotia incisa*. These species are all indicative of acidobiontic to acidophilous conditions (e.g. Stevenson *et al.*, 1991). Species associated with slightly higher alkalinity (c.5 mg l⁻¹) and pH (6.3-6.7) include acidophilous taxa such as *Tabellaria flocculosa* and *Brachysira vitrea*. More circumneutral streams with relatively high alkalinity (5-30 mg l⁻¹) and pH (c.7) are dominated by *Achnanthes minutissima*, with *Gomphonema [angustatum/parvulum]*, *Fragilaria vaucheriae* and *Achnanthes saxonica* also common. The very high alkalinity sites (> 40 mg l⁻¹) with high pH (>7.5) are characterised by *Achnanthes minutissima* and *Cocconeis placentula* with *Amphora pediculus* and *Cymbella sinuata* also common. Several other species are important in specific groups of samples (e.g. *Diatoma hyemale* is associated with COINSPAN Group 5a).

This clear relationship between diatom assemblages and surface water acidity is well documented in the literature (e.g. ter Braak & van Dam 1989, Stevenson *et al.* 1991, Battarbee 1994, van Dam 1996), and has also been clearly established for epilithic diatoms in upland streams. In a study of epilithic diatoms in streams in Belgium, for example, Leclercq (1977) stressed the importance of acidity in determining assemblage composition and species distributions. Juggins (1992) also found stream-water pH to be the most important factor controlling epilithic diatom assemblages in a series of 149 Scottish streams. This study confirms such findings, and demonstrates that the most important influence on the epilithic

Figure 8 Boxplot of distribution of pH across the stream sample COINSPAN groups



diatom assemblages in the Welsh stream dataset is alkalinity and co-variables.

In addition to the pH/alkalinity gradient, the DCA and CCA reveal several other significant chemical variables. The most notable of these (see Table 3) is Fe, but the Monte Carlo permutation tests within the forward selection procedure indicate that Mn, Mg, Na and TON-N also show significant, independent relationships with the diatom data. These latter relationships are difficult to interpret with clarity, and may be a result of the noisy structure of the data or the tendency for over-selection of variables within the CANOCO forward selection procedure (see ter Braak & Verdonschot 1995). The relationship with Fe, however, is better defined, with several species (e.g. *Eunotia meisteri*, *Eunotia exigua* and *Cymbella lunata*) associated with samples with high Fe concentrations. The influence of Fe (and to some extent Mn) is also apparent in the COINSPAN analysis. Groups 1, 3b and 4 are all associated with elevated levels of these metals, and all contain high abundances of *Eunotia exigua*. Diatom response to surface water metal concentrations, independently of acidity, have been noted by several authors (see Dixit *et al.* 1992). In particular, *Eunotia exigua* is known to be tolerant of elevated metal concentrations. For example, Besch *et al.* (1972) reported the dominance of this species in mine waste polluted streams, and van Dam and Mertens (1990) reported its importance in Lake Orta, a metal contaminated lake in Italy. It is also possible that the relationship between the diatom assemblages and Fe reflects redox conditions rather than a response to metals *per se*.

A further strong gradient of variation in the diatom data is associated with certain of the catchment variables. It is clear from the variance partitioning (Table 6) that the forward selected catchment variables explain a significant amount of the variation in diatom data independently from the between-sample variation in chemistry that might be controlled by catchment factors (e.g. the very high alkalinity sites are associated with brown earth soils - COINSPAN Group 7). This is most clearly reflected in the second DCA axis, which is strongly correlated with %conifer and catchment gradient in particular (see Table 3). Sites with high %conifer and gradient are associated with small, firmly attached (adnate) species such as *Achnanthes austriaca* var. *helvetica*, *Eunotia vanheurckii* var. *intermedia* and *Eunotia* [sp. 10(*minima*)]. Sites with low gradient and %conifer are associated with species such as *Tabellaria flocculosa* and *Eunotia nagelii*, and more loosely attached pendunculate (stalked) taxa. This pattern is also apparent in the second CCA axis, although the pattern is less distinct than in the DCA due to the additional influence of Fe on CCA axis 2, and in the COINSPAN analysis. COINSPAN Group 2 is associated with high catchment gradients with *Eunotia exigua* and *Eunotia vanheurckii* var. *intermedia* important taxa, and COINSPAN groups 3b and 4 are both associated with low catchment gradients and an abundance of *Tabellaria flocculosa*.

These patterns are interpreted as the influence of stream-water flow conditions and current velocity on diatom assemblages. In fast flowing, high velocity upland streams there is generally a greater representation of firmly attached forms (e.g. Cox 1990a, Sabater & Roca 1990, Round 1993), and larger stalked forms are restricted due to high shear-stress. Although no direct data is available on local flow characteristics at the sampling sites, it seems reasonable to assume a correlation between catchment gradient and stream-water flow conditions within the dataset. The samples dominated by the small adnate forms (e.g. *Eunotia vanheurckii* var. *intermedia*) therefore most probably represent fast flowing systems, whereas the samples which contain larger, pendunculate, sometimes colonial forms such as *Tabellaria flocculosa* probably come from more slowly flowing streams or reaches. These relationships are probably also responsible for some of the other significant relationships between the assemblages and catchment variables. The relationship with %conifer, for example, is similar to the relationship with gradient and may reflect the flow characteristics of forested catchments, although it is also possible that shading effects influence the diatom assemblages in conifer forests (e.g. Stockner

& Armstrong 1971). This latter hypothesis is difficult to test with the current dataset, which lacks information on shading at the sample sites.

The analyses also show a relatively minor, but statistically significant, relationship between the diatom assemblages and sampling period (see Table 6). There are therefore significant differences between the assemblages of the diatom assemblages of the spring and summer samples which are independent of changes in chemical conditions. This variation is associated with two species in particular, both of which occur in intermediate to high alkalinity samples. *Gomphonema* [*angustatum/parvulum*] is associated with spring samples and is most abundant in the samples from COINSPAN Group 5a, whereas *Synedra miniscula* is associated with summer samples and is most abundant in COINSPAN groups 3b and 5b. The potential importance of seasonality on epilithic diatom assemblages has been discussed by several authors (e.g. Cox 1990a, 1990b), but is generally more prevalent in higher alkalinity systems. Moore (1977), for example, observed seasonal variation in the abundance of *Synedra* species in a high alkalinity, lowland river. In contrast studies in more acid systems have shown a lack of significant seasonal response in diatom assemblages (e.g. Jones & Flower 1986). However, it is clear from the current study that seasonal variability is an important factor influencing diatom assemblages at the higher alkalinity sites.

4 Lake samples

4.1 Diatom occurrence and abundance

Figure 9 shows the relationship between diatom occurrence and maximum abundance in the lake samples. *Achnanthes minutissima* and *Tabellaria flocculosa* plot in the top right hand corner, and represent taxa which occur in a high proportion of the samples and can dominate the assemblages. *Achnanthes marginulata* can also be dominant, but occurs in fewer samples. The data also include a series of species relatively abundant in many of the samples (e.g. *Eunotia naegelii*, *Eunotia incisa*, *Fragilaria vaucheriae*), and species which are abundant in relatively few samples (e.g. *Eunotia vanheurckii* var. *intermedia*, *Achnanthes austriaca* var. *minor*, *Diatoma hyemale*). The majority of taxa plot in the lower left corner of the plot, and occur in low abundance in relatively few samples. Table 8 shows the frequency distribution of N_2 sample diversity for the lake samples. N_2 diversity is generally low in comparison to lake sediment diatom assemblages (N_2 typically 5-20, Juggins 1992) but 60% of the samples have $N_2 > 4$. Few of the samples can be considered species poor (e.g. $N_2 < 2$).

Table 8 Frequency distribution of N_2 sample diversity for lake samples

N_2 diversity	0-2	2-4	4-6	6-8	8-10	>10
No. of samples	4	9	8	6	4	1

4.2 Detrended correspondence analysis (DCA)

DCA analysis was performed for exploration of the main gradients of floristic variation in the lake diatom samples. Detrending was by third order polynomials (ter Braak 1990b). The DCA shows one dominant axis ($\lambda_1 = 0.599$) which explains 17.5% of the variance in diatom data (Table 9). This first axis is strongly correlated with variables representative of acid-base status, most notably alkalinity ($r = 0.790$) and pH ($r = 0.776$). Samples with low axis 1 scores include IRDA, DULA, and MANOB, and are associated with acidophilous and acidobiontic species such as *Achnanthes marginulata*, *Navicula leprostriata* and *Peronia fibula* (see Figures 10 and 11). Samples with high scores on this axis are associated with more acidophilous to circumneutral taxa such as *Achnanthes minutissima*, *Achnanthes saxonica*, *Cymbella microcephala* and *Navicula jaernfeltii*. The axis clearly represents a floristic gradient associated with lake-water acidity

Figure 9 Scatterplot of diatom occurrence and maximum abundance in the lake samples

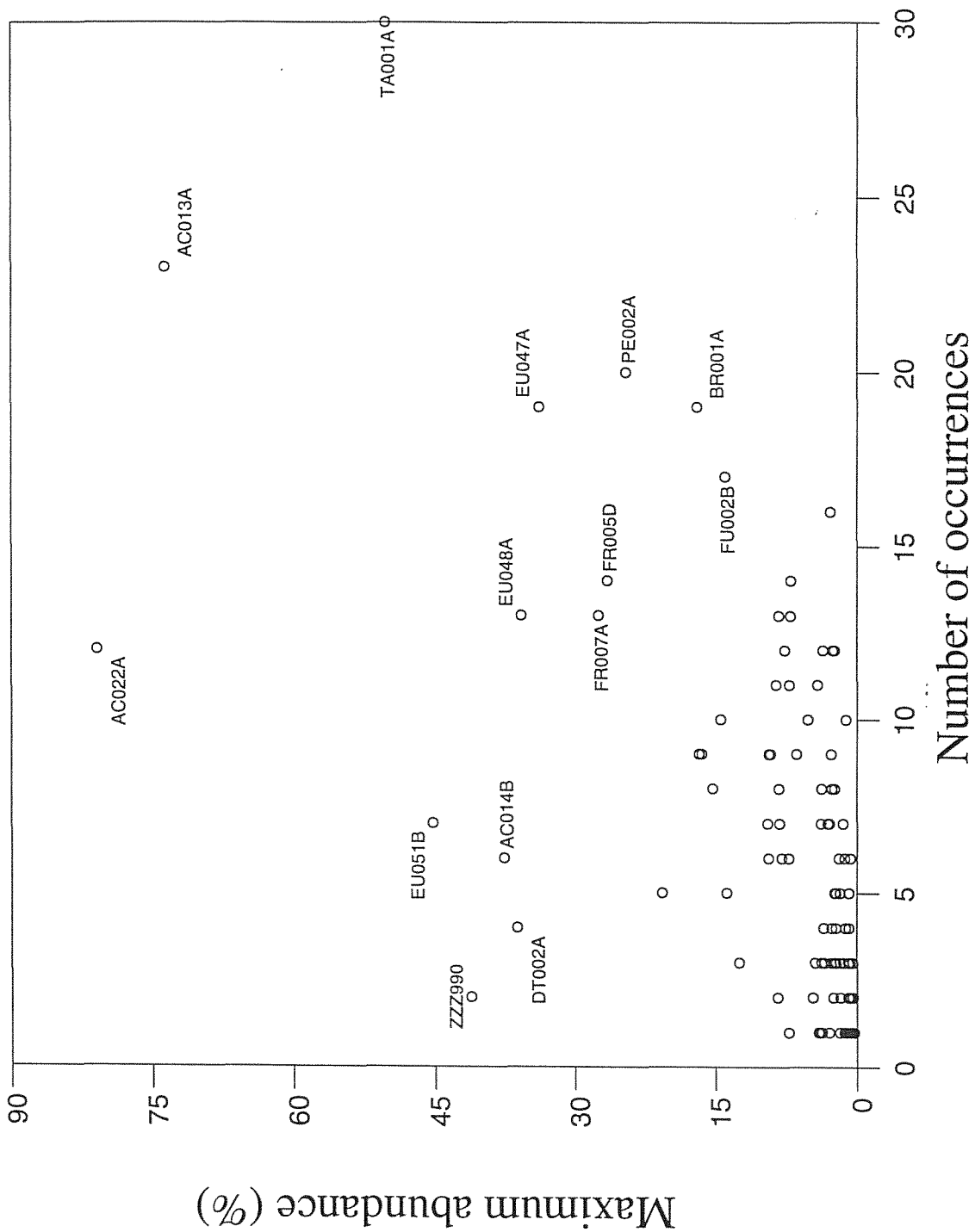


Figure 10 DCA sample plot for lake samples

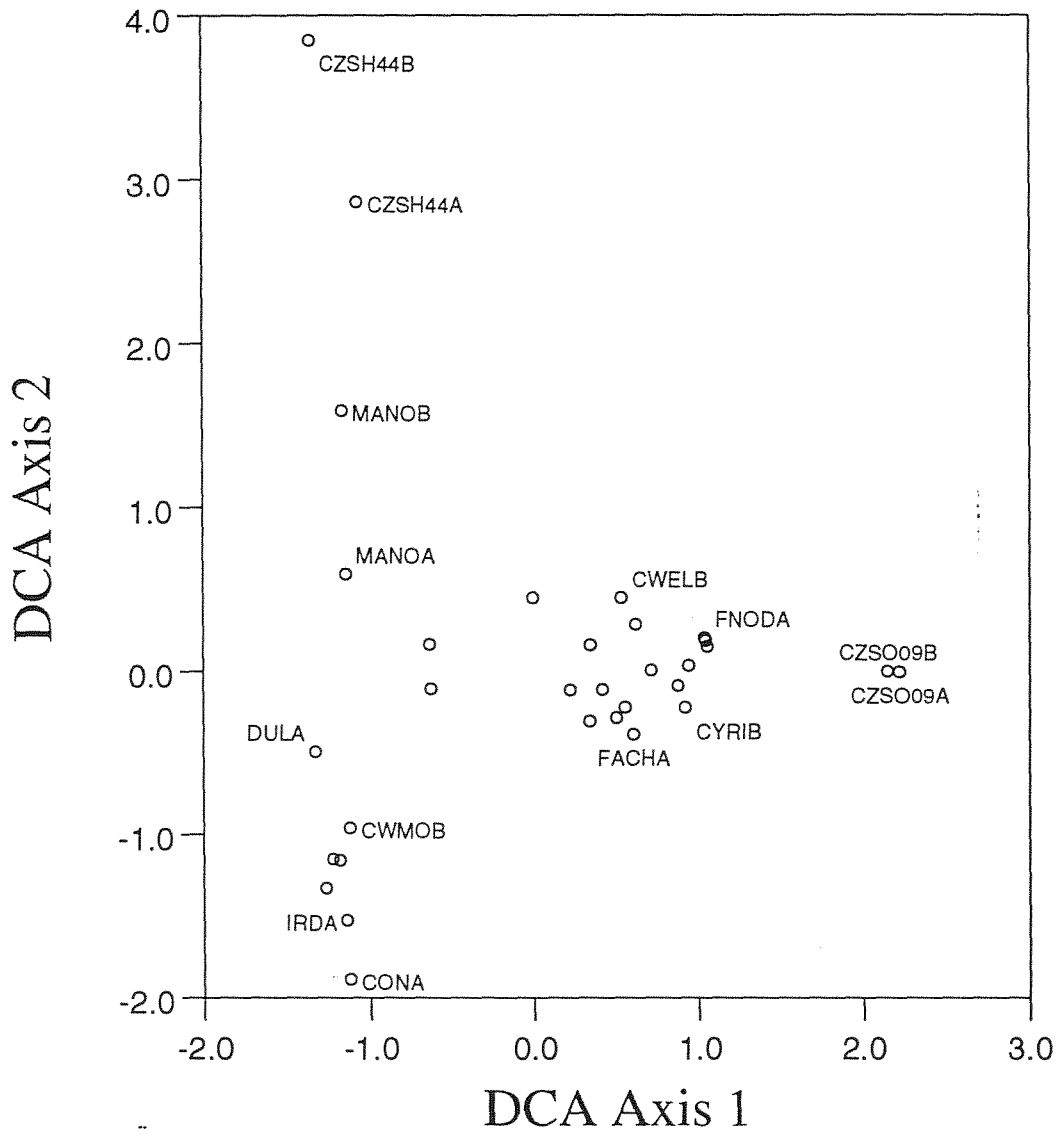
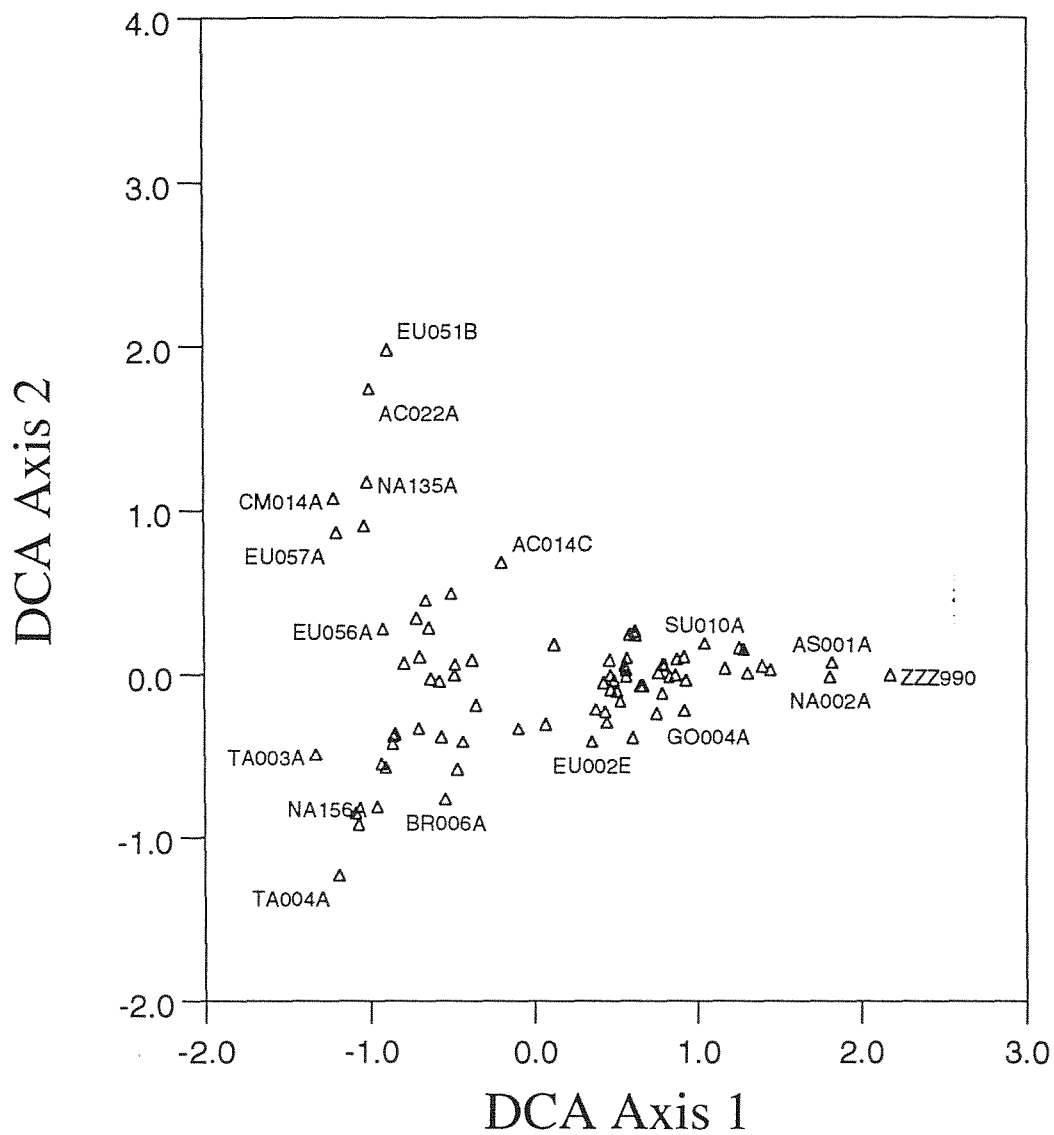


Figure 11 DCA species plot for lake samples



The second DCA axis is less important ($\lambda_2 = 0.316$), but still explains 9.1% of the variation in the diatom data. The axes separates samples with low axis 1 scores (Figure 10). CZSH44B, CZSH44A and MANOB have high scores on axis 2, and these samples are particularly associated with *Achnanthes marginulata*, *Achnanthes austriaca* var. *helvetica*, *Navicula tenuicephala* and *Eunotia vanheurckii* var. *intermedia*. Conversely samples with low axis 2 scores are also dominated by acidophilous to acidobiontic taxa, but characterised by high abundances of *Tabellaria quadrisepata*, *Eunotia naegelii*, *Tabellaria flocculosa*, *Brachysira vitrea* and *Navicula leptostriata*. The axis is difficult to interpret, but is correlated with the proportion of Stagno-podzol soils in the catchment. The axis seems to distinguish between samples dominated by smaller, generally adnate (attached) diatoms (e.g. small *Achnanthes*) and samples which also contain larger, pendunculate (stalked) taxa (e.g. *Tabellaria quadrisepata*).

DCA axes 3 and 4 explain relatively little of the variance in diatom data, and more importantly contain no coherent, interpretable pattern of variation in the diatom data.

Table 9 DCA results for the 32 lake samples, where r is the correlation between environmental variables and the ordination axis. Only statistically significant values ($p \leq 0.05$) are shown for selected environmental variables

	DCA axis 1	DCA axis 2	DCA axis 3	DCA axis 4
Eigenvalue	0.599	0.316	0.237	0.135
Variance explained	17.5 %	9.1 %	6.9 %	4.0 %
pH	r=0.776	-	-	-
Alkalinity	r=0.790	-	-	-
Hardness	r=0.690	-	r=-0.403	-
Ca	r=0.605	-	-	-
Conductivity	r=0.471	-	-	-
Hardness	r=0.690	-	-	-
K	r=0.666	-	-	-
Na	-	-	-	r=0.440
%StagPod	-	r=0.359	r=-0.362	-

4.3 Canonical correspondence analysis (CCA)

CCA was performed on the lake sample dataset to directly explore the relationship between diatom assemblages and environmental variables. The forward selection option within CANOCO was used to identify a minimal, independently significant set of explanatory variables (ter Braak 1990b) (see Table 10). A subset of five environmental variables were identified that each explain a significant ($P \leq 0.05$) proportion of the variance in diatom data. The most important explanatory variables are pH and K, which together account for 58% of the variance explained by the five forward selected variables.

Results of CCA analysis using the five selected variables are shown in Table 11 and Figures 12 and 13. The first CCA axis ($\lambda_1 = 0.539$) explains 15.7% of the variance in diatom data, and is strongly correlated with pH ($r = 0.742$) and K ($r = 0.763$). The second axis explains 11.3% of the variance, and is negatively correlated with pH ($r = -0.557$) and catchment gradient ($r = -0.558$). These first two axes are both significant on the basis of Monte Carlo permutation tests ($P < 0.01$, 499 permutations). Samples from site CZSO09 are clearly shown as outliers on the basis of the first two axes, plotting in the top right of Figure 12 and associated with taxa largely absent from other samples (e.g. *Achnanthes detha*, *Navicula jaernfeltii*, *Nitzschia* [cf. *palea*] and *Navicula* [cf. *subrotunda*]) (Figure 13). These two samples also have very high concentrations of lake-water K compared to other samples, and this variable significantly influences the CCA. The first two axes also distinguish between two other groupings of sites; those with low axis 1 scores (e.g. CZSH44A, IRDB), and those with intermediate axis 1 and low axis 2 scores (e.g. CZSH93B, YROEA) (Figure 12). This division is associated with a gradient of pH. The first grouping contains samples with relatively low pH, and is associated with acidophilous to acidobiontic taxa such as *Eunotia naegelii*, *Eunotia incisa* and *Navicula leptostriata*. The second grouping contains samples with relatively high pH associated with acidophilous to circumneutral taxa such as *Achnanthes minutissima*, *Fragilaria construens* var. *venter* and *Nitzschia austriaca*.

The third CCA axis explains 8.0% of the variance in diatom data, and is strongly correlated with %conifer. The axis is significant ($P < 0.01$, 499 permutations) and essentially isolates the two samples from site SYFY (which has high %conifer). These samples are associated with high proportions of the taxa *Achnanthes austriaca* var. *minor* and *Navicula difficillima*. The fourth CCA axis is not significant on the basis of Monte Carlo permutations tests.

Figure 12 CCA sample-environmental variable biplot for lake samples

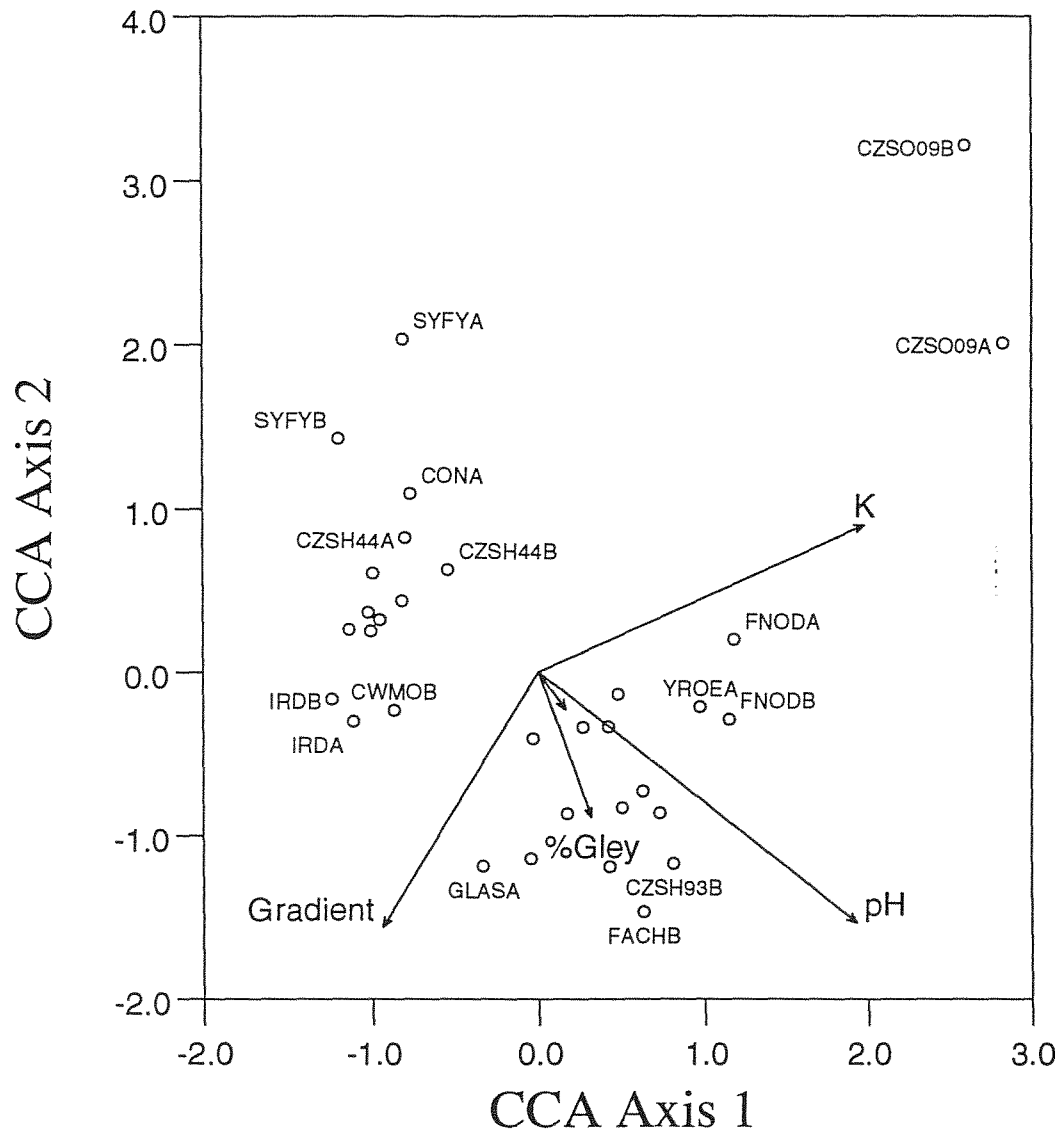


Figure 13 CCA species-environmental variable biplot for lake samples

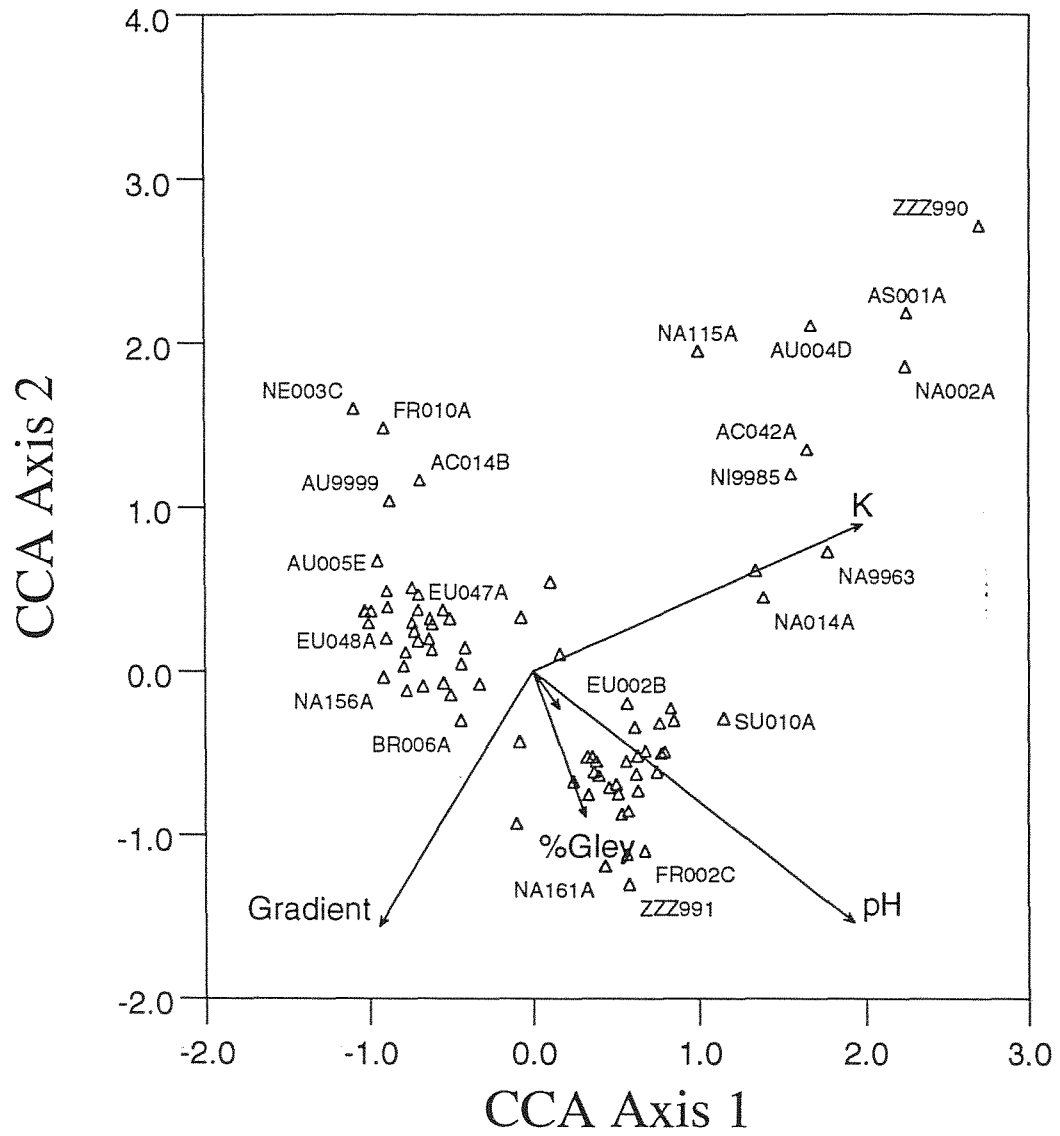


Table 10 Variance potentially explained by selected environmental variables before forward selection and variance explained with the addition of each environmental variable during forward selection in CCA of the lake sample data.

Variable	Before forward selection	Added with selection
pH	0.47	0.47
K	0.45	0.36
%Conifer	0.21	0.21
%Gley	0.17	0.20
Gradient	0.22	0.18
Alkalinity	0.39	
Hardness	0.37	
Ca	0.31	
Conductivity	0.25	
TON-N	0.22	
Al	0.18	
	Sum of variance	1.42

Table 11 CCA results for the 32 lake samples, where r is the correlation between environmental variables and the ordination axis. Only statistically significant values ($p \leq 0.05$) are shown for the forward selected environmental variables.

	CCA axis 1	CCA axis 2	CCA axis 3	CCA axis 4
Eigenvalue	0.539	0.389	0.275	0.129
Variance explained	15.7 %	11.3 %	8.0 %	3.8 %
pH	$r=0.742$	$r=-0.557$	-	-
K	$r=0.763$	-	-	-
%Conifer	-	-	$r=0.704$	$r=0.361$
Gradient	$r=-0.364$	$r=-0.558$	-	-
%Gley	-	-	-	$r=0.764$

4.4 COINSPAN sample classification

The COINSPAN classification of the lake samples is shown in Figure 14, which indicates the mean abundance of common taxa in each COINSPAN group. Four groups of samples were identified at two levels of division, and six subgroups at three levels of division. The first division is strongly associated with pH, and recognises the circumneutral taxon *Achnanthes minutissima* as a positive indicator (e.g. preferential to Groups 3 and 4). The second division isolates the two samples from site SYFY into Group 1 on the basis of the negative indicator *Achnanthes austriaca* var. *minor*, and is associated with %Conifer. Similarly, the third division isolates the two samples from site CZSO09 with high values of lake-water K into Group 4, with *Achnanthes minutissima* as a negative indicator (preferential to Group 3). Group 2 is divided into subgroups on the basis of the indicator taxon *Eunotia naegelii* (preferential to subgroup 2a), effectively segregating the two samples from site CZSH44 into subgroup 2b. Group 3 is subdivided on the basis of the indicator taxon *Cymbella microcephala* (preferential to subgroup 3b). Table 12 shows the mean values of the forward selected environmental variables in the lake sample COINSPAN groups.

Figure 14

COINSPAN classification of lake samples, showing mean abundance of common taxa in each group

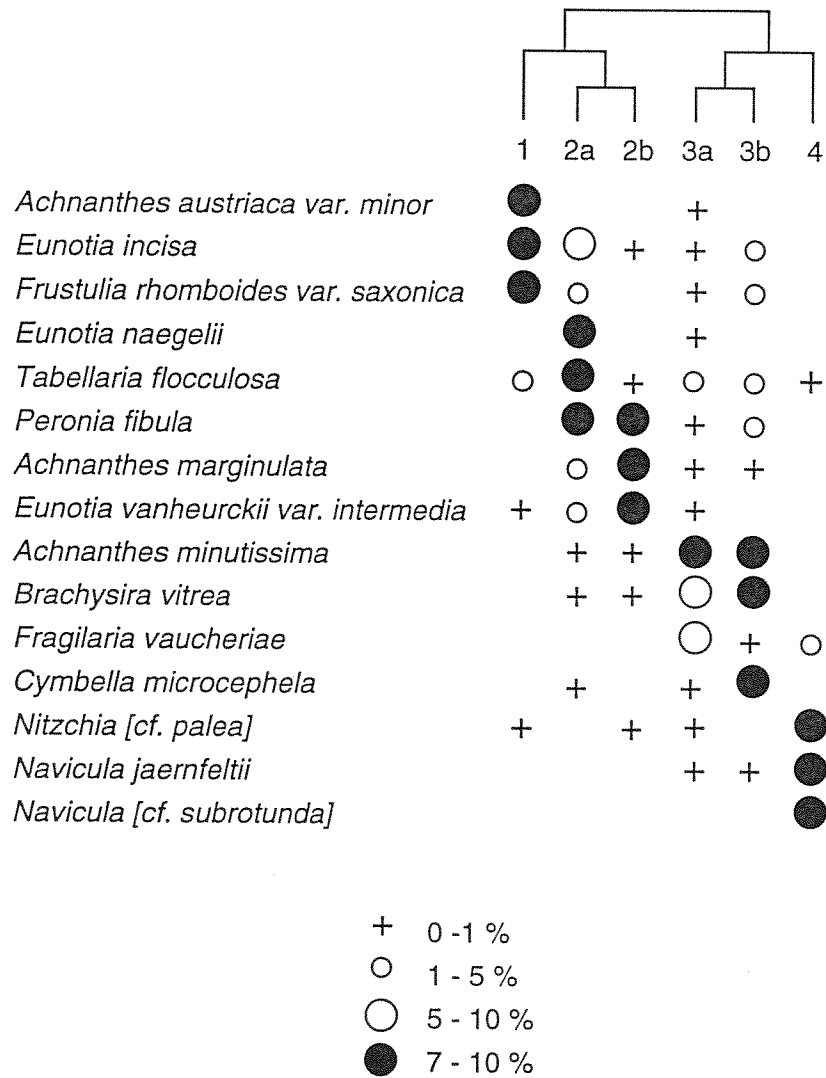


Table 12 Mean values of forward selected environmental variables in the lake sample COINSPAN groups. Figure in parentheses represent standard deviations.

COINSPAN group	1	2a	2b	3a	3b	4
no. of samples	2	9	2	14	3	2
pH	4.95 (-)	5.39 (0.21)	5.42 (-)	6.51 (0.19)	6.05 (0.93)	6.23 (-)
K	0.16 (-)	0.16 (0.08)	0.43 (-)	0.32 (0.17)	0.41 (0.31)	1.67 (-)
%Conifer	54.5 (-)	0 (0)	0 (-)	2.27 (2.74)	35.8 (31.0)	0 (-)
Gradient	5 (-)	14.1 (4.2)	17.1 (-)	13.8 (6.3)	9.9 (5.4)	2.4 (-)
%Gley	0 (-)	0.01 (0.02)	0 (-)	0.01 (0.01)	0.15 (0.07)	0.01 (-)

The COINSPAN groups for the lake samples can be summarised according to their species composition and environmental characteristics.

COINSPAN Group 1 *Achnanthes austriaca* var. *minor*/*Eunotia incisa*

Characterised by *Achnanthes austriaca* var. *minor*, but *Eunotia incisa* is also abundant and *Frustulia rhomboides* var. *saxonica* and *Fragilaria constrict* are common. Contains the two samples from site SYFY, which has very low pH and a high proportion of conifer afforestation in the catchment.

COINSPAN Group 2a *Eunotia naegelii*/*Tabellaria flocculosa*/*Eunotia incisa*

Characterised by high abundances of *Eunotia naegelii*, with *Tabellaria flocculosa*, *Eunotia incisa* and *Peronia fibula* also abundant. Other common taxa include *Achnanthes marginulata*, *Tabellaria quadriseptata* and *Eunotia vanheurckii* var. *intermedia*. The samples have relatively low lake-water pH (typically 5.2 - 5.6).

COINSPAN Group 2b *Achnanthes marginulata*/*Eunotia vanheurckii* var. *intermedia*

This subgroup contains the two samples from site CZSH44 which contain diatom assemblages dominated by *Achnanthes marginulata*, *Peronia fibula* and *Eunotia vanheurckii* var. *intermedia*. The site has relatively low lake-water pH.

COINSPAN Group 3a *Achnanthes minutissima/Brachysira vitrea/Tabellaria flocculosa*

Dominated by *Achnanthes minutissima*, with *Brachysira vitrea* and *Tabellaria flocculosa* also common. *Fragilaria virescens* var. *exigua* and *Fragilaria vaucheriae* are present. These samples have relatively high lake-water pH (mean value 6.51).

COINSPAN Group 3b *Achnanthes minutissima/Cymbella microcephela*

Dominated by *Achnanthes minutissima* and characterised by the presence of *Cymbella microcephela*. *Brachysira vitrea* and *Fragilaria virescens* var. *exigua* are also common, and the more acidophilous *Peronia fibula*, *Tabellaria flocculosa* and *Eunotia incisa* are present in low abundance. The mean pH value for the samples is 6.05.

COINSPAN Group 4 *Nitzschia [cf. palea]/Navicula jaernfeltii*

This group contains the two samples from site CZSO09, which have relatively high lake-water pH and elevated concentrations of lake-water K (see Table 12). The samples are characterised by *Nitzschia [cf. palea]*, *Navicula jaernfeltii* and *Navicula [cf. subrotunda]*.

4.5 Discussion

The lake samples contain relatively diverse assemblages when compared to the samples in the stream dataset. This reflects the influence of flow and current velocity on stream assemblages, and the more stable conditions and diverse microhabitats available for colonisation by diatoms on stones in lake systems. In particular, lake epilithon samples have a higher proportion of stalked (penduculate) or colonial forms which can be restricted in fast flowing streams (Round 1993). Stones in lake systems can also become covered with layers of mucilage or substantive algal growths, increasing the potential microhabitats available for different forms of diatoms (Round 1981). The lake samples generally contain species common to epilithic assemblages in dilute lakes indicative of acidophilous (e.g. *Eunotia incisa*, *Achnanthes margimulata*, *Tabellaria flocculosa*, *Peronia fibula*, *Brachysira vitrea*) to circumneutral (e.g. *Achnanthes minutissima*, *Cymbella microcephela*) conditions. In a study of Welsh lakes Allott & Juggins (1991) identified a very similar range of species occurrence. Round (1990a, 1990b) has also studied epilithic diatoms in Welsh lakes, and identified two discreet assemblage types; firstly, assemblages in acid lakes dominated by *Eunotia incisa-Tabellaria flocculosa*, and secondly assemblages in higher pH lakes dominated by *Achnanthes minutissima*. This distinction largely reflects the important division in the current dataset between COINSPAN Group 2 and COINSPAN Group 3. However, the dataset also contains samples dominated by other taxa, namely the samples in Group 1 (*Achnanthes austriaca* var. *minor*) and Group 4 (*Nitzschia [cf. palea]* and *Navicula jaernfeltii*).

The diatom assemblages can be related to those in the 11 Acid Waters Monitoring Network lakes (Patrick *et al.* 1991, Patrick *et al.* 1995). The assemblages of COINSPAN Group 3a (*Achnanthes minutissima/Brachysira vitrea/Tabellaria flocculosa*) closely correspond to the assemblages in several of the AWMN lakes with pH in the range 6.0 - 6.5 (e.g. Loch Coire nan Arr, Loch Tinker, Burnmoor Tarn). In addition, the assemblages of COINSPAN Group 2b reflect those of Lochnagar, both

containing very high proportions of *Achnanthes marginulata*. However, the remaining AWMN sites contain assemblages not represented in the Welsh lake dataset. These sites are characterised by high abundances of either *Eunotia incisa* (e.g. Loch Grannoch, Scoat Tarn, Llyn Llagi, Llyn Cwm Mynach) or the acidobiontic *Tabellaria quadrisepitata* (e.g. Round Loch of Glenhead, Blue Loch). These sites represent the most acid sites in the AWMN (pH < 5.2). Such very acid sites are not well represented in this Welsh dataset.

The data analyses show that the dominant gradient in diatom data in the lake sample dataset is associated with lake-water acidity. The first DCA axis is strongly correlated with pH, alkalinity and co-variables (Table 9), and reflects a gradient from sites containing acidobiontic-acidophilous taxa (e.g. *Achnanthes marginulata*, *Navicula leptostriata* and *Peronia fibula*) to sites associated with more circumneutral taxa (e.g. *Achnanthes minutissima*). This gradient is also apparent in the first CCA axis (Table 11) and the COINSPAN groups (Table 12), and reflects the established influence of acidity on diatom assemblages (e.g. Stevenson *et al.* 1991). Interpretation of other influences on the assemblages is more difficult due to the small number of samples in the dataset, and the 'noisy' characteristics of the diatom data. These factors have resulted in assemblages from individual sites having a strong influence on the multivariate analyses. This effect is illustrated by the samples from sites CZSO09 and SYFY, both of which have atypical assemblages within the dataset as a whole. In the CCA and COINSPAN analyses the association of these sets of samples with high lake-water K and %conifer respectively is accentuated, resulting in apparent significant relationships between these variables and the total variance in diatom data. In such a restricted dataset such relationships may be statistically significant, but cannot be interpreted with confidence in terms of **ecological** significance.

In addition to the acidity gradient, the DCA ordination reveals a second important pattern of variation in diatom data. This is the division within the relatively low pH, acidophilous assemblages between samples dominated by small, adnate taxa (e.g. *Achnanthes marginulata* and *Achnanthes austriaca* var. *minor*; COINSPAN Groups 1 and 2b) and those containing a larger proportion of stalked (pendunculate) forms and taxa such as *Eunotia nagelii* and *Tabellaria flocculosa* (COINSPAN Group 2a). This division is not represented in the CCA analysis, suggesting that it is not associated with any of the environmental variables included in the analysis. As the division seems to be related to the life-forms of taxa it may be associated with the degree of turbulence in the littoral zone of the lakes, possibly as a result of exposure or fetch. However, this hypothesis is impossible to test with the data available.

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Appendix A Site and sample codes

NRA Code	UCL Code	Grid Reference	Sitename	Sample Code	Date	Site Type
25228	CON	SH782456	LLYN CONWY	CONA	4/11/95	L
25228	CON	SH782456	LLYN CONWY	CONB	7/12/95	L
23160	CWEL	SH552556	LLYN CWELLYN	CWELA	4/12/95	L
23160	CWEL	SH552556	LLYN CWELLYN	CWELB	7/11/95	L
23168	CWMO	SH679460	LLYN CWMORTHIN	CWMOA	4/11/95	L
23168	CWMO	SH679460	LLYN CWMORTHIN	CWMOB	7/11/95	L
25457	CYRI	SH657117	LLYN CYRI	CYRIA	4/10/95	L
25457	CYRI	SH657117	LLYN CYRI	CYRIE	7/10/95	L
25456	CZSH44	SH493495	LLYN CWM DULYN	CZSH44A	4/12/95	L
25456	CZSH44	SH493495	LLYN CWM DULYN	CZSH44B	7/10/95	L
3140	CZSH93	SH929397	LLYN MAEN BRAS	CZSH93A	4/10/95	L
3140	CZSH93	SH929397	LLYN MAEN BRAS	CZSH93B	7/10/95	L
39263	CZSO09	SO020975	LLYN TARW	CZSO09A	4/13/95	L
39263	CZSO09	SO020975	LLYN TARW	CZSO09B	7/12/95	L
25453	DUL	SH662244	LLYN DULYN	DULA	4/10/95	L
25453	DUL	SH662244	LLYN DULYN	DULB	7/10/95	L
71681	FACH	SN905037	LLYN FACH	FACHA	4/11/95	L
71681	FACH	SN905037	LLYN FACH	FACHB	7/11/95	L
89170	FNOD	SN603643	LLYN FANOD	FNODA	4/13/95	L
89170	FNOD	SN603643	LLYN FANOD	FNODB	7/12/95	L
25454	GLAS	SH601547	LLYN GLAS	GLASA	4/11/95	L
25454	GLAS	SH601547	LLYN GLAS	GLASB	7/11/95	L
25455	IRD	SH630220	LLYN IRDDYN	IRDA	4/10/95	L
25455	IRD	SH630220	LLYN IRDDYN	IRDB	7/10/95	L
23166	MANO	SH718452	LLYN MANOD	MANOA	4/11/95	L
23166	MANO	SH718452	LLYN MANOD	MANOB	7/11/95	L
35258	SYFY	SN723847	LLYN SYFYDRIM	SYFYA	4/13/95	L
35258	SYFY	SN723847	LLYN SYFYDRIM	SYFYB	7/12/95	L
191	W001	SH879311	DYFRDWY	W001A	4/24/95	S
191	W001	SH879311	DYFRDWY	W001B	7/30/95	S
280	W002	SH838398	TRYWERYN	W002A	4/05/95	S
280	W002	SH838398	TRYWERYN	W002B	7/19/95	S
305	W003	SH920562	ALWEN	W003A	4/05/95	S
305	W003	SH920562	ALWEN	W003B	7/17/95	S
336	W004	SH978587	FECHAN	W004A	4/05/95	S
336	W004	SH978587	FECHAN	W004B	7/17/95	S
2662	W005	SH918585	NANT Y FOEL DDU	W005A	4/05/95	S
2662	W005	SH918585	NANT Y FOEL DDU	W005B	7/17/95	S
3142	W006	SH974213	HIRDDU	W006A	4/06/95	S
3142	W006	SH974213	HIRDDU	W006B	7/11/95	S
3143	W007	SH989183	COWNWY	W007A	4/06/95	S
3143	W007	SH989183	COWNWY	W007B	7/11/95	S
3144	W008	SH944135	BANWY	W008A	4/06/95	S
3144	W008	SH944135	BANWY	W008B	7/11/95	S
3145	W009	SJ072295	DISGYNFA	W009A	4/06/95	S
3145	W009	SJ072295	DISGYNFA	W009B	7/11/95	S
20274	W010	SH751320	HIR	W010A	4/07/95	S
20274	W010	SH751320	HIR	W010B	7/19/95	S
20276	W011	SH749323	GANOL	W011A	4/07/95	S
20276	W011	SH749323	GANOL	W011B	7/19/95	S
20277	W012	SH755335	GAIN	W012A	4/07/95	S
20277	W012	SH755335	GAIN	W012B	7/19/95	S
20279	W013	SH778104	CEISWYN	W013A	4/24/95	S
20279	W013	SH778104	CEISWYN	W013B	7/12/95	S
20280	W014	SH779105	DULAS N.	W014A	4/24/95	S
20280	W014	SH779105	DULAS N.	W014B	7/12/95	S
20282	W015	SH765104	LLEFENNI	W015A	4/12/95	S
20282	W015	SH765104	LLEFENNI	W015B	4/24/95	S
20284	W016	SH744089	CWM EIDDEW	W016A	4/24/95	S
20284	W016	SH744089	CWM EIDDEW	W016B	7/12/95	S
20285	W017	SH690078	NANT IAGO	W017A	7/12/95	S
20285	W017	SH690078	NANT IAGO	W017B	7/24/95	S
20286	W018	SH825164	CERIST	W018A	4/03/95	S
20286	W018	SH825164	CERIST	W018B	7/21/95	S
20287	W019	SH791196	HELYGOG	W019A	4/06/95	S
20287	W019	SH791196	HELYGOG	W019B	7/20/95	S
20288	W020	SH816224	HARNOG	W020A	4/06/95	S
20288	W020	SH816224	HARNOG	W020B	7/20/95	S
20289	W021	SH817229	WNION	W021A	4/06/95	S
20289	W021	SH817229	WNION	W021B	7/20/95	S
20310	W022	SH788293	MAWDDACH	W022A	4/07/95	S
20310	W022	SH788293	MAWDDACH	W022B	7/20/95	S
20311	W023	SH774297	BRYN LLIN MAWR	W023A	4/07/95	S
20311	W023	SH774297	BRYN LLIN MAWR	W023B	7/20/95	S
20312	W024	SH768289	CEIRW	W024A	4/07/95	S
20312	W024	SH768289	CEIRW	W024B	7/20/95	S
23173	W025	SH747418	CYNFAL	W025A	4/05/95	S
23173	W025	SH747418	CYNFAL	W025B	7/19/95	S

23174	W026	SH751428	PISTYLL	W026A	4/05/95	S
23174	W026	SH751428	PISTYLL	W026B	7/19/95	S
23175	W027	SH630514	CWM Y LLAN	W027A	4/04/95	S
23175	W027	SH630514	CWM Y LLAN	W027B	7/18/95	S
23176	W028	SH576509	COLWYN	W028A	4/04/95	S
23176	W028	SH576509	COLWYN	W028B	7/18/95	S
23177	W029	SH573500	TRIB OF COLWYN	W029A	4/03/95	S
23177	W029	SH573500	TRIB OF COLWYN	W029B	7/18/95	S
25234	W030	SH788506	GLASCWM	W030A	4/04/95	S
25234	W030	SH788506	GLASCWM	W030B	7/17/95	S
25237	W031	SH700572	NANT Y GWRYD	W031A	4/04/95	S
25237	W031	SH700572	NANT Y GWRYD	W031B	7/18/95	S
25238	W032	SH718580	LLUGWY	W032A	4/04/95	S
25238	W032	SH718580	LLUGWY	W032B	7/18/95	S
25239	W033	SH737522	CWMPENAMNEN	W033A	4/04/95	S
25239	W033	SH737522	CWMPENAMNEN	W033B	7/17/95	S
25240	W034	SH711516	LLEDR	W034A	4/04/95	S
25240	W034	SH711516	LLEDR	W034B	7/17/95	S
25241	W035	SH779446	AFON CONWY	W035A	4/05/95	S
25241	W035	SH779446	AFON CONWY	W035B	7/19/95	S
25242	W036	SH857494	CALETTWR	W036A	4/05/95	S
25242	W036	SH857494	CALETTWR	W036B	7/17/95	S
25451	W037	SH633262	CWM NANTCOL	W037A	4/03/95	S
25451	W037	SH633262	CWM NANTCOL	W037B	7/19/95	S
25452	W038	SH683209	CWM MYNACH	W038A	4/03/95	S
25452	W038	SH683209	CWM MYNACH	W038B	7/20/95	S
34408	W039	SN718675	MEURIG	W039A	4/21/95	S
34408	W039	SN718675	MEURIG	W039B	7/21/95	S
35206	W040	SN744767	MYNACH	W040A	4/21/95	S
35206	W040	SN744767	MYNACH	W040B	7/06/95	S
35270	W041	SN767868	NANT Y MOCH INPUT	W041A	4/26/95	S
35270	W041	SN767868	NANT Y MOCH INPUT	W041B	7/10/95	S
35644	W042	SN789737	NANT MILWYN	W042A	4/21/95	S
35644	W042	SN789737	NANT MILWYN	W042B	7/06/95	S
39257	W043	SN870891	BIGA	W043A	3/28/95	S
39257	W043	SN870891	BIGA	W043B	7/21/95	S
39258	W044	SN872905	LLWYD	W044A	3/28/95	S
39258	W044	SN872905	LLWYD	W044B	7/21/95	S
39259	W045	SN904952	TRANNON	W045A	3/28/95	S
39259	W045	SN904952	TRANNON	W045B	7/12/95	S
39261	W046	SO190670	CWM Y GERWYN	W046A	3/25/95	S
39261	W046	SO190670	CWM Y GERWYN	W046B	7/21/95	S
39260	W047	SO144520	TRIB OF GLAS BROOK	W047A	3/25/95	S
39260	W047	SO144520	TRIB OF GLAS BROOK	W047B	6/19/95	S
39262	W048	SO109488	TRIB OF EDW	W048A	3/25/95	S
39262	W048	SO109488	TRIB OF EDW	W048B	6/19/95	S
40867	W049	SN851254	STR@SN851254	W049A	3/30/95	S
40867	W049	SN851254	STR@SN851254	W049B	6/21/95	S
40881	W050	SN925207	SENNI	W050A	3/30/95	S
40881	W050	SN925207	SENNI	W050B	6/21/95	S
40889	W051	SN972223	STR@SN972223	W051A	3/30/95	S
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57000	W052	SN824841	BLAENCYFF	W052A	4/27/95	S
57000	W052	SN824841	BLAENCYFF	W052B	7/06/95	S
57001	W053	SN823821	CELLIOGYN	W053A	4/27/95	S
57001	W053	SN823821	CELLIOGYN	W053B	7/06/95	S
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57002	W054	SN877822	BIDNO	W054B	7/06/95	S
57003	W055	SN888799	TROEDYRESGAIR	W055A	4/27/95	S
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57004	W056	SN890722	HIRIN	W056B	7/07/95	S
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57005	W057	SN889723	ELAN	W057B	7/07/95	S
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70085	W059	SS843903	SYCHBANT	W059B	6/22/95	S
71072	W060	SS805905	WERNDERI	W060A	3/28/95	S
71072	W060	SS805905	WERNDERI	W060B	6/27/95	S
71073	W061	SS873994	NANT DU	W061A	3/28/95	S
71073	W061	SS873994	NANT DU	W061B	6/22/95	S
71682	W062	SN972165	LLIA	W062A	3/30/95	S
71682	W062	SN972165	LLIA	W062B	6/21/95	S
72159	W063	SN676089	STR@SN676089	W063A	3/27/95	S
72159	W063	SN676089	STR@SN676089	W063B	6/27/95	S
72160	W064	SN791129	GIEDD	W064A	3/28/95	S
72160	W064	SN791129	GIEDD	W064B	6/22/95	S
72161	W065	SN792128	NANT CYW	W065A	3/28/95	S
72161	W065	SN792128	NANT CYW	W065B	6/22/95	S
72758	W066	SN735143	AMMAN	W066A	3/28/95	S
72758	W066	SN735143	AMMAN	W066B	6/27/95	S
81068	W067	SN778889	HENGWM	W067A	4/26/95	S
81068	W067	SN778889	HENGWM	W067B	7/10/95	S
88085	W068	SN822497	LLYN BRIANNE LI5	W068A	3/31/95	S
88085	W068	SN822497	LLYN BRIANNE LI5	W068B	6/19/95	S
88111	W069	SN805488	LLYN BRIANNE LI8	W069A	3/31/95	S

88111	W069	SN805488	LLYN BRIANNE LI8	W069B	6/19/95	S
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88116	W070	SN782464	TRIB OF TYWI	W070B	6/19/95	S
89101	W071	SN754910	TRIB LLECHWEDD MAWR 1	W071A	4/26/95	S
89102	W072	SN754908	TRIB LLECHWEDD MAWR 2	W072A	4/26/95	S
89103	W073	SN742886	STR@SN742886	W073A	4/26/95	S
89103	W073	SN742886	STR@SN742886	W073B	7/10/95	S
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89105	W075	SN733833	STR@SN733833	W075B	7/07/95	S
89106	W076	SN743818	STR@SN743818	W076A	4/26/95	S
89106	W076	SN743818	STR@SN743818	W076B	7/07/95	S
89112	W077	SN775748	PEIRAN	W077A	4/19/95	S
89112	W077	SN775748	PEIRAN	W077B	7/06/95	S
89113	W078	SN762729	TRIB OF YSTWYTH	W078A	4/19/95	S
89113	W078	SN762729	TRIB OF YSTWYTH	W078B	7/06/95	S
89119	W079	SN694597	BERWYN	W079A	4/21/95	S
89119	W079	SN694597	BERWYN	W079B	7/03/95	S
89120	W080	SN694599	GROES	W080A	4/21/95	S
89120	W080	SN694599	GROES	W080B	7/03/95	S
89121	W081	SN681545	BREFI	W081A	4/21/95	S
89121	W081	SN681545	BREFI	W081B	7/03/95	S
89122	W082	SN644516	CLYWEDOG U	W082A	4/18/95	S
89122	W082	SN644516	CLYWEDOG U	W082B	7/03/95	S
89123	W083	SN769656	EGNANT	W083A	4/19/95	S
89123	W083	SN769656	EGNANT	W083B	7/21/95	S
89124	W084	SN769655	MWYRO	W084A	4/19/95	S
89124	W084	SN769655	MWYRO	W084B	7/21/95	S
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89130	W085	SN511395	IAR	W085B	7/05/95	S
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89131	W086	SN517400	CEILIOG	W086B	7/05/95	S
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89132	W087	SN518402	CEREDIG	W087B	7/05/95	S
89133	W088	SN524417	CYNHENFOD	W088A	4/20/95	S
89133	W088	SN524417	CYNHENFOD	W088B	6/28/95	S
89134	W089	SN525420	HUST	W089A	4/20/95	S
89134	W089	SN525420	HUST	W089B	6/28/95	S
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89142	W094	SN707483	COTHI UPPER	W094B	6/20/95	S
89143	W095	SN715469	TRIB OF COTHI	W095A	4/18/95	S
89143	W095	SN715469	TRIB OF COTHI	W095B	6/20/95	S
89144	W096	SN703438	NANT DAR	W096A	4/19/95	S
89144	W096	SN703438	NANT DAR	W096B	6/20/95	S
89145	W097	SN685504	TWRCH UPPER	W097A	4/20/95	S
89145	W097	SN685504	TWRCH UPPER	W097B	7/05/95	S
89147	W098	SN699400	DULAIS	W098A	4/19/95	S
89147	W098	SN699400	DULAIS	W098B	6/20/95	S
89148	W099	SN692437	TRIB OF COTHI@SN692437	W099A	4/19/95	S
89148	W099	SN692437	TRIB OF COTHI@SN692437	W099B	6/26/95	S
89149	W100	SN679405	ANNELL	W100A	4/19/95	S
89149	W100	SN679405	ANNELL	W100B	6/20/95	S
89202	W101	SN078305	PRESELI 3	W101A	3/27/95	S
89202	W101	SN078305	PRESELI 3	W101B	6/26/95	S
89203	W102	SN078309	PRESELI 4	W102A	3/27/95	S
89203	W102	SN078309	PRESELI 4	W102B	6/26/95	S
89204	W103	SN073314	PRESELI 5	W103A	3/27/95	S
89204	W103	SN073314	PRESELI 5	W103B	6/26/95	S
89206	W104	SN056338	PRESELI 10	W104A	3/27/95	S
89206	W104	SN056338	PRESELI 10	W104B	6/26/95	S
23161	YGAD	SH568524	LLYN GADAIR	YGADA	6/23/95	L
23161	YGAD	SH568524	LLYN GADAIR	YGADB	7/11/95	L
89171	YROE	SN728798	LLYN YR OERFA	YROEA	4/13/95	L
89171	YROE	SN728798	LLYN YR OERFA	YROEB	7/12/95	L

Appendix B

Diatom taxa, codes and authorities for stream samples

Code	Taxon	Date	Authority
AC001A	<i>Achnanthes lanceolata</i>	1880	(Breb. ex Kutz.) Grun. in Cleve & Grun.
AC002A	<i>Achnanthes linearis</i>	1880	(W. Sm.) Grun. in Cleve & Grun.
AC002B	<i>Achnanthes linearis curta</i>	1916	H.L. Sm. ex Boyer
AC004A	<i>Achnanthes pseudoswazi</i>	1963	J.R. Carter
AC013A	<i>Achnanthes minutissima minutissima</i>	1833	Kutz.
AC014B	<i>Achnanthes austriaca minor</i>	1986	L. Grannoch (RJF)
AC014C	<i>Achnanthes austriaca helvetica</i>	1933	Hust.
AC022A	<i>Achnanthes marginulata</i>	1880	Grun. in Cleve & Grun.
AC023A	<i>Achnanthes conspicua conspicua</i>	1919	A. Mayer
AC024A	<i>Achnanthes depressa</i>	1933	(Cleve) Hust.
AC028A	<i>Achnanthes saxonica</i>	1933	Krasske in Hust.
AC035A	<i>Achnanthes pusilla pusilla</i>	1880	Grun. in Cleve & Grun.
AC042A	<i>Achnanthes detha</i>		
AC048A	<i>Achnanthes scotica</i>		Jones & Flower
AC148A	<i>Achnanthes modestiformis</i>		Lange-Bertalot
AC152A	<i>Achnanthes carissima</i>		Lange-Bertalot
AC9975	<i>Achnanthes [altaica var. minor]</i>	1988	L. Grannoch (RJF)
AC9996	<i>Achnanthes cf. levanderi</i>		
AC9999	<i>Achnanthes sp.</i>		
AM012A	<i>Amphora pediculus</i>		(Kutz.) Grun.
AS001A	<i>Asterionella formosa formosa</i>	1850	Hassall
AU005D	<i>Aulacoseira distans tenella</i>	1986	(Nygaard) R. Ross in Hartley
AU005E	<i>Aulacoseira distans nivalis</i>		
AU010B	<i>Aulacoseira perglabra floriniae</i>		
AU9999	<i>Aulacoseira sp.</i>		
BR001A	<i>Brachysira vitrea</i>	1986	(Grun.) R. Ross in Hartley
BR003A	<i>Brachysira serians</i>	1981	(Breb. ex Kutz.) Round & Mann
BR006A	<i>Brachysira brebissonii brebissonii</i>	1986	R. Ross in Hartley
CA002A	<i>Caloneis bacillum bacillum</i>	1894	(Grun.) Cleve
CA018A	<i>Caloneis tenuis</i>	1985	Gregory (Krammer)
CM003A	<i>Cymbella sinuata sinuata</i>	1856	Greg.
CM004A	<i>Cymbella microcephala microcephala</i>	1880	Grun. in Van Heurck
CM009A	<i>Cymbella naviculiformis</i>	1863	Auersw. ex Heib.
CM010A	<i>Cymbella perpussilla</i>	1895	A. Cleve
CM012A	<i>Cymbella laevis</i>	1849	Naegeli ex Kutz.
CM014A	<i>Cymbella aequalis</i>	1855	W. Sm. ex Grev.
CM017A	<i>Cymbella hebridica</i>	1894	(Grun. ex Cleve) Cleve
CM022A	<i>Cymbella affinis</i>	1844	Kutz.
CM031A	<i>Cymbella minuta minuta</i>	1862	Hilse ex Rabenh.
CM038A	<i>Cymbella delicatula</i>	1849	Kutz.
CM048A	<i>Cymbella lunata</i>	1855	W. Sm. in Grev.
CM084A	<i>Cymbella lacustre</i>	1849	(Ag.) Kutz.
CM9999	<i>Cymbella sp.</i>		
CO001A	<i>Cocconeis placentula placentula</i>	1838	Ehrenb.
CO010A	<i>Cocconeis disculus</i>	1896	(Schum.) Cleve
CY006A	<i>Cyclotella kuetzingiana kuetzingiana</i>	1848	Thwaites
DD001A	<i>Digyosphenia geminata</i>	1899	(Lyngb.) M. Schmidt in A. Schmidt
DE001A	<i>Denticula tenuis tenuis</i>	1844	Kutz.
DI001A	<i>Diatomella balfouriana balfouriana</i>	1855	Grev.
DP001A	<i>Diploneis ovalis</i>	1894	(Hilse) Cleve
DT002A	<i>Diatoma hyemale hyemale</i>	1863	(Roth) Heib.
DT004B	<i>Diatoma tenue elongatum</i>	1819	Lyngb.
EP003A	<i>Epithemia argus argus</i>	1844	(Ehrenb.) Kutz.
EU002A	<i>Eunotia pectinalis pectinalis</i>	1864	(O.F. Mull.) Rabenh.
EU002B	<i>Eunotia pectinalis minor</i>	1864	(Kutz.) Rabenh.
EU002C	<i>Eunotia pectinalis ventralis</i>	1911	(Ehrenb.) Hust.
EU002E	<i>Eunotia pectinalis minor impressa</i>		(Ehr.) Hust.
EU003A	<i>Eunotia praerupta praerupta</i>	1843	Ehrenb.
EU004A	<i>Eunotia tenella</i>	1895	(Grun. in Van Heurck) A. Cleve
EU009A	<i>Eunotia exigua exigua</i>	1864	(Breb. ex Kutz.) Rabenh.
EU011A	<i>Eunotia rhomboidea</i>	1950	Hust.
EU015A	<i>Eunotia denticulata denticulata</i>	1864	(Breb. ex Kutz.) Rabenh.
EU016A	<i>Eunotia diodon</i>	1837	Ehrenb.
EU017A	<i>Eunotia flexuosa flexuosa</i>	1849	Kutz.
EU020A	<i>Eunotia meisteri meisteri</i>	1930	Hust.
EU021A	<i>Eunotia sudetica</i>	1898	O. Mull.
EU022A	<i>Eunotia bigibba bigibba</i>	1849	Kutz.
EU025A	<i>Eunotia fallax</i>	1895	A. Cleve
EU026A	<i>Eunotia praerupta-nana</i>		Berg
EU027A	<i>Eunotia trinacria trinacria</i>	1929	Krasske
EU028B	<i>Eunotia microcephala tridentata</i>		(A. Mayer) Hust.
EU029A	<i>Eunotia valida</i>	1930	Hust.
EU040A	<i>Eunotia paludosa</i>	1862	Grun.
EU043A	<i>Eunotia elegans</i>	1910	Ostr.
EU045A	<i>Eunotia nymanniana</i>	1881	Grun. in Van Heurck
EU047A	<i>Eunotia incisa</i>	1854	W. Sm. ex Greg.
EU048A	<i>Eunotia naegelii</i>	1907	Migula
EU049A	<i>Eunotia curvata curvata</i>	1884	(Kutz.) Lagerst.
EU049B	<i>Eunotia curvata subarcuata</i>	1954	(Naegeli ex Kutz.) Woodhead & Tweed
EU049D	<i>Eunotia curvata attenuata</i>		A. Berg (Cleve Euler)
EU051A	<i>Eunotia vanheurckii vanheurckii</i>	1958	Patr.
EU051B	<i>Eunotia vanheurckii intermedia</i>		(Krasske) Cleve
EU053A	<i>Eunotia tridentula</i>	1843	Ehrenb.
EU053B	<i>Eunotia tridentula perminuta</i>	1881	Grun. in Van Heurck
EU056A	<i>Eunotia minutissima</i>	1934	A. Cleve-Euler
EU057A	<i>Eunotia exgracilis</i>	1953	A. Berg ex A. Cleve-Euler
EU9961	<i>Eunotia [vanheurckii var. 1]</i>	1988	Round L. Glenhead (RJF)
EU9965	<i>Eunotia [sp. 10 (minima)]</i>	1988	L. Grannoch (RJF)
EU9999	<i>Eunotia sp.</i>		
FR001A	<i>Fragilaria pinnata pinnata</i>	1843	Ehrenb.
FR002A	<i>Fragilaria construens construens</i>	1862	(Ehrenb.) Grun.

FR002E	Fragilaria construens binodis	1862	(Ehrenb.) Grun.
FR002C	Fragilaria construens venter	1881	(Ehrenb.) Grun. in Van Heurck
FR005A	Fragilaria virescens virescens	1843	Ralfs
FR005D	Fragilaria virescens exigua	1881	Grun. in Van Heurck
FR006A	Fragilaria brevistriata brevistriata	1885	Grun. in Van Heurck
FR007A	Fragilaria vaucheriae vaucheriae	1938	(Kutz.) J.B. Petersen
FR010A	Fragilaria constricta constricta	1843	Ehrenb.
FR9999	Fragilaria sp.		
FU001A	Frustulia vulgaris vulgaris	1891	(Thwaites) De Toni
FU002A	Frustulia rhomboides rhomboides	1891	(Ehrenb.) De Toni
FU002B	Frustulia rhomboides saxonica	1891	(Rabenh.) De Toni
FU002F	Frustulia rhomboides viridula	1894	(Breb. ex Kutz.) Cleve
GO001A	Gomphonema olivaceum	1838	(Hornemann) Breb.
GO003B	Gomphonema angustatum productum	1880	Grun. in Van Heurck
GO004A	Gomphonema gracile	1838	Ehrenb.
GO005A	Gomphonema lagerheimi	1895	A. Cleve
GO006C	Gomphonema acuminatum coronatum	1853	(Ehrenb.) W. Sm.
GO014A	Gomphonema intricatum	1844	Kutz.
GO014B	Gomphonema intricatum pumilum	1880	Grun. in Van Heurck
GO017A	Gomphonema lanceolatum		Ehr.
GO024C	Gomphonema clevei	1902	Fricke in A. Schmidt
GO9999	Gomphonema sp.		
HNO01A	Hannaea arcus arcus	1966	(Ehrenb.) Patr. in Patr. & Reimer
MR001A	Meridion circulare circulare	1831	(Grev.) Ag.
NA002A	Navicula jaernefeltii	1942	Hust.
NA003A	Navicula radiosa radiosa	1844	Kutz.
NA003E	Navicula radiosa tenella	1885	(Breb. ex Kutz.) Grun. ex Van Heurck
NA006A	Navicula medicocris	1932	Krasske
NA007A	Navicula cryptocephala cryptocephala	1844	Kutz.
NA008A	Navicula rhyncocephala rhyncocephala	1844	Kutz.
NA014A	Navicula pupula pupula	1844	Kutz.
NA016A	Navicula indifferens	1942	Hust.
NA018A	Navicula wittrockii	1934	(Lagerst.) A. Cleve-Euler
NA021A	Navicula cincta	1861	(Ehrenb.) Ralfs in Pritch.
NA023A	Navicula gregaria	1861	Donk.
NA025A	Navicula mutica mutica	1844	Kutz.
NA029A	Navicula gracilis	1830	Ehrenb.
NA033A	Navicula subtilissima	1891	Cleve
NA037A	Navicula angusta	1860	Grun.
NA038A	Navicula arvensis		Hust.
NA039A	Navicula festiva	1925	Krasske
NA042A	Navicula minima minima	1880	Grun. in Van Heurck
NA044A	Navicula krasskei	1930	Hust.
NA045A	Navicula bryophila bryophila	1928	J.B. Petersen
NA046A	Navicula contenta contenta	1885	Grun. in Van Heurck
NA058A	Navicula phyllepta	1844	Kutz.
NA064A	Navicula exilis	1844	Kutz.
NA086A	Navicula tantula	1943	Hust.
NA112A	Navicula minuscula minuscula	1880	Grun. in Van Heurck
NA135A	Navicula tenuicephala	1942	Hust.
NA138A	Navicula pelliculosa	1862	(Kutz.) Hilse in Rabenh.
NA149A	Navicula digitulus	1943	Hust.
NA156A	Navicula leptostriata	1948	Jorgensen
NA158A	Navicula cumbriensis	1987	Haworth
NA162A	Navicula avenacea	1878	(Breb. & Godey) Breb. ex Grun.
NA577A	Navicula porifera	1944	Hust.
NA9939	Navicula [cf. minima]	1987	Oresjon (IR-SWAP)
NA9963	Navicula [sp. 1]	1986	L. Hir (SF)
NA9999	Navicula sp.		
NE004A	Neidium bisulcatum bisulcatum	1894	(Lagerst.) Cleve
NE006A	Neidium alpinum	1943	Hust.
NE020A	Neidium hercynicum	1917	A. Mayer
NE9999	Neidium sp.		
NI002A	Nitzschia fonticola	1881	Grun. in Van Heurck
NI005A	Nitzschia perminuta	1903	(Grun. in Van Heurck) M. Perag.
NI008A	Nitzschia frustulum	1880	(Kutz.) Grun. in Cleve & Grun.
NI015A	Nitzschia dissipata	1862	(Kutz.) Grun.
NI017A	Nitzschia gracilis	1860	Hantzsch
NI020A	Nitzschia angustata angustata	1880	(W. Sm.) Grun. in Cleve & Grun.
NI020B	Nitzschia angustata acuta	1880	Grun. in Cleve & Grun.
NI025A	Nitzschia recta	1861	Hantzsch ex Rabenh.
NI033A	Nitzschia paleacea	1881	(Grun. in Cleve & Grun.) Grun. in Van He
NI9985	Nitzschia [cf. palea]	1988	Uisge (VJJ)
NI9999	Nitzschia sp.		
PE002A	Peronia fibula	1956	(Breb. ex Kutz.) R. Ross
PI007A	Pinnularia viridis viridis	1843	(Nitzsch) Ehrenb.
PI008A	Pinnularia divergens divergens	1853	W. Sm.
PI011A	Pinnularia microstauron microstauron	1891	(Ehrenb.) Cleve
PI012A	Pinnularia borealis	1843	Ehrenb.
PI015A	Pinnularia abaujensis abaujensis	1986	(Pant.) R. Ross in Hartley
PI018A	Pinnularia biceps biceps	1856	Greg.
PI022A	Pinnularia subcapitata subcapitata	1856	Greg.
PI022B	Pinnularia subcapitata hilseana	1898	(Janisch ex Rabenh.) O. Mull.
PI023A	Pinnularia irrorata	1939	(Grun. in Van Heurck) Hust.
PI024A	Pinnularia stomatophora stomatophora	1891	(Grun. ex A. Schmidt) Cleve
PI030A	Pinnularia acoricola		Hust.
PI9999	Pinnularia sp.		
SA001A	Stauroneis anceps anceps	1843	Ehrenb.
SA001E	Stauroneis anceps gracilis	1864	Rabenh.
SA9999	Stauroneis sp.		
SP002A	Stenopterobia sigmatella	1986	(Greg.) R. Ross in Hartley
SU003A	Surirella ovalis ovalis	1838	Breb.
SU004A	Surirella biseriata biseriata	1835	Breb. & Godey
SU006A	Surirella delicatissima delicatissima	1864	Lewis
SU9999	Surirella sp.		
SY001A	Synedra ulna ulna	1836	(Nitzsch) Ehrenb.
SY002A	Synedra rumpens rumpens	1844	Kutz.
SY003A	Synedra acus acus	1844	Kutz.
SY010A	Synedra minuscula	1881	Grun. in Van Heurck

SY043A	Synedra famelica	1844	Kutz.
SY9999	Synedra sp.	1844	(Roth) Kutz.
TA001A	Tabellaria flocculosa flocculosa		Koppen
TA001B	Tabellaria flocculosa flocculosa IIIp	1881	(Ehrenb.) Grun. in Van Heurck
TA003A	Tabellaria binalis	1952	Knudson
TA004A	Tabellaria quadrisepitata		Lange-Bertalot
TA005A	Tabellaria kutzingiana		
UN9998	Unknown naviculaceae		
UN9999	Unknown		
ZZZ992	Achnanthes [cf. doenensis]		
ZZZ993	Eunotia arculus		
ZZZ994	Nitzschia diversa		
ZZZ995	Nitzschia lacuum		
ZZZ996	Achnanthes [cf. strenzkii]		
ZZZ998	Achnanthes biasoletiana		
ZZZ999	Gomphonema [angustatum/parvulum]		

Appendix C

Diatom taxa, codes and authorities for lake samples

Code	Taxon	Date	Authority
AC002A	Achnanthes linearis	1880	(W. Sm.) Grun. in Cleve & Grun.
AC002B	Achnanthes linearis curta	1916	H.L. Sm. ex Boyer
AC004A	Achnanthes pseudoswazi	1963	J.R. Carter
AC013A	Achnanthes minutissima minutissima	1833	Kutz.
AC014B	Achnanthes austriaca minor	1986	L. Grannoch (RJF)
AC014C	Achnanthes austriaca helvetica	1933	Hust.
AC022A	Achnanthes marginulata	1880	Grun. in Cleve & Grun.
AC024A	Achnanthes depressa	1933	(Cleve) Hust.
AC028A	Achnanthes saxonica	1933	Krasske in Hust.
AC034A	Achnanthes suchlandtii	1933	Hust.
AC035A	Achnanthes pusilla pusilla	1880	Grun. in Cleve & Grun.
AC039A	Achnanthes didyma didyma	1933	Hust.
AC042A	Achnanthes detha		
AC046A	Achnanthes altaica	1953	(Poretzky) A. Cleve-Euler
AC048A	Achnanthes scotica		Jones & Flower
AC9969	Achnanthes [scotica/marginulata]	1988	Groningen (RJF)
AC9975	Achnanthes [altaica var. minor]	1988	L. Grannoch (RJF)
AC9996	Achnanthes cf. levanderi		
AC9999	Achnanthes sp.		
AS001A	Asterionella formosa formosa	1850	Hassall
AS003A	Asterionella ralfsii	1856	W. Sm.
AU004D	Aulacoseira lirata alpigena		(Grun.) Haworth
AU005B	Aulacoseira distans nivaloides	1987	Camburn
AU005E	Aulacoseira distans nivalis		
AU010A	Aulacoseira perglabra		
AU010B	Aulacoseira perglabra floriniae		
AU9999	Aulacoseira sp.		
BR001A	Brachysira vitrea	1986	(Grun.) R. Ross in Hartley
BR006A	Brachysira brebissonii brebissonii	1986	R. Ross in Hartley
CM004A	Cymbella microcephala microcephala	1880	Grun. in Van Heurck
CM010A	Cymbella perpusilla	1895	A. Cleve
CM013A	Cymbella helvetica helvetica	1844	Kutz.
CM014A	Cymbella aequalis	1855	W. Sm. ex Grev.
CM017A	Cymbella hebridica	1894	(Grun. ex Cleve) Cleve
CM031A	Cymbella minuta minuta	1862	Hilse ex Rabenh.
CM047A	Cymbella incerta	1878	Grun. in Cleve & Moller
CM048A	Cymbella lunata	1855	W. Sm. in Grev.
CM052A	Cymbella descripta	1985	(Hust.) Krammer & Lange-Bertalot
CM9999	Cymbella sp.		
CY004A	Cyclotella stelligera	1882	(Cleve & Grun. in Cleve) Van Heurck
CY006A	Cyclotella kuetzingiana kuetzingiana	1848	Thwaites
CY006D	Cyclotella kuetzingiana minor		nov. nom.
DT002A	Diatoma hyemale hyemale	1863	(Roth) Heib.
EU002A	Eunotia pectinalis pectinalis	1864	(O.F. Mull.) Rabenh.
EU002B	Eunotia pectinalis minor	1864	(Kutz.) Rabenh.
EU002C	Eunotia pectinalis ventralis	1911	(Ehrenb.) Hust.
EU002E	Eunotia pectinalis minor impressa		(Ehr.) Hust.
EU004A	Eunotia tenella	1895	(Grun. in Van Heurck) A. Cleve
EU007A	Eunotia bigentula	1856	W. Sm.
EU009A	Eunotia exigua exigua	1864	(Breb. ex Kutz.) Rabenh.
EU011A	Eunotia rhomboidea	1950	Hust.
EU015A	Eunotia denticulata denticulata	1864	(Breb. ex Kutz.) Rabenh.
EU021A	Eunotia sudetica	1898	O. Mull.
EU026A	Eunotia praerupta-nana		Berg
EU027A	Eunotia trinacria trinacria	1929	Krasske
EU028B	Eunotia microcephala tridentata		(A. Mayer) Hust.
EU029A	Eunotia valida	1930	Hust.
EU040A	Eunotia paludosa	1862	Grun.
EU045A	Eunotia nymanniana	1881	Grun. in Van Heurck
EU047A	Eunotia incisa	1854	W. Sm. ex Greg.
EU048A	Eunotia naegelii	1907	Migula
EU049A	Eunotia curvata curvata	1884	(Kutz.) Lagerst.
EU049B	Eunotia curvata subarcuata	1954	(Naegeli ex Kutz.) Woodhead & Tweed
EU049D	Eunotia curvata attenuata		A. Berg (Cleve Euler)
EU051A	Eunotia vanheurckii vanheurckii	1958	Patr.
EU051B	Eunotia vanheurckii intermedia		(Krasske) Cleve
EU053B	Eunotia tridentula perminuta	1881	Grun. in Van Heurck
EU056A	Eunotia minutissima	1934	A. Cleve-Euler
EU057A	Eunotia exgracilis	1953	A. Berg ex A. Cleve-Euler
EU9999	Eunotia sp.		
FR001A	Fragilaria pinnata pinnata	1843	Ehrenb.
FR002A	Fragilaria construens construens	1862	(Ehrenb.) Grun.
FR002C	Fragilaria construens venter	1881	(Ehrenb.) Grun. in Van Heurck
FR005A	Fragilaria virescens virescens	1843	Ralfs
FR005D	Fragilaria virescens exigua	1881	Grun. in Van Heurck
FR006A	Fragilaria brevistriata brevistriata	1885	Grun. in Van Heurck
FR007A	Fragilaria vaucheriae vaucheriae	1938	(Kutz.) J.B. Petersen
FR010A	Fragilaria constricta constricta	1843	Ehrenb.
FR018A	Fragilaria elliptica	1867	Schum.
FR9991	Fragilaria [cf. oldenburgiana PIRLA pl 20, 61]	1987	PIRLA
FR9999	Fragilaria sp.		
FU001A	Frustulia vulgaris vulgaris	1891	(Thwaites) De Toni
FU002B	Frustulia rhomboides saxonica	1891	(Rabenh.) De Toni
FU002F	Frustulia rhomboides viridula	1894	(Breb. ex Kutz.) Cleve
GO004A	Gomphonema gracile	1838	Ehrenb.
GO006C	Gomphonema acuminatum coronatum	1853	(Ehrenb.) W. Sm.
GO010B	Gomphonema constrictum capitatum	1885	(Ehrenb.) Grun. in Van Heurck
GO014B	Gomphonema intricatum pumilum	1880	Grun. in Van Heurck
GO019A	Gomphonema augur		Ehr.
GO9999	Gomphonema sp.		

NA002A	Navicula jaernefeltii	1942	Hust.
NA003A	Navicula radiosa radiosa	1844	Kutz.
NA003B	Navicula radiosa tenella	1885	(Breb. ex Kutz.) Grun. ex Van Heurck
NA006A	Navicula medicocris	1932	Krasske
NA006B	Navicula medicocris atomus		Hust.
NA007A	Navicula cryptocephala cryptocephala	1844	Kutz.
NA013A	Navicula pseudoscutiformis	1930	Hust.
NA014A	Navicula pupula pupula	1844	Kutz.
NA032A	Navicula cocconeiformis cocconeiformis	1855	Greg. ex Greville
NA033A	Navicula subtilissima	1891	Cleve
NA037A	Navicula angusta	1860	Grun.
NA042A	Navicula minima minima	1880	Grun. in Van Heurck
NA044A	Navicula krasskei	1930	Hust.
NA045A	Navicula bryophila bryophila	1928	J.B. Petersen
NA068A	Navicula impexa	1961	Hust.
NA084A	Navicula atomus	1860	(Kutz.) Grun.
NA115A	Navicula difficillima	1950	Hust.
NA133A	Navicula schassmannii	1937	Hust.
NA135A	Navicula tenuicephala	1942	Hust.
NA156A	Navicula leptostriata	1948	Jorgensen
NA158A	Navicula cumbriensis	1987	Haworth
NA160A	Navicula submolesta	1949	Hust.
NA161A	Navicula absoluta	1950	Hust.
NA167A	Navicula hoefleri		Sensu Ross et Sims
NA9963	Navicula [sp. 1]	1986	L. Hir (SF)
NA9999	Navicula sp.		
NE003C	Neidium affine amphirhynchus	1894	(Ehrenb.) Cleve
NE006A	Neidium alpinum	1943	Hust.
NE020A	Neidium hercynicum	1917	A. Mayer
NI002A	Nitzschia fonticola	1881	Grun. in Van Heurck
NI005A	Nitzschia perminuta	1903	(Grun. in Van Heurck) M. Perag.
NI017A	Nitzschia gracilis	1860	Hantzsch
NI025A	Nitzschia recta	1861	Hantzsch ex Rabenh.
NI9985	Nitzschia [cf. palea]	1988	Uisge (VJJ)
NI9999	Nitzschia sp.		
PE002A	Peronia fibula	1956	(Breb. ex Kutz.) R. Ross
PI011A	Pinnularia microstauron microstauron	1891	(Ehrenb.) Cleve
PI015A	Pinnularia abaujensis abaujensis	1986	(Pant.) R. Ross in Hartley
PI018A	Pinnularia biceps biceps	1856	Greg.
PI022A	Pinnularia subcapitata subcapitata	1856	Greg.
PI022B	Pinnularia subcapitata hilseana	1898	(Janisch ex Rabenh.) O. Mull.
PI023A	Pinnularia irrorata	1939	(Grun. in Van Heurck) Hust.
PI9999	Pinnularia sp.		
SA001A	Stauroneis anceps	1843	Ehrenb.
SA001B	Stauroneis anceps gracilis	1864	Rabenh.
SP002A	Stenopterobia sigmatella	1986	(Greg.) R. Ross in Hartley
SU004A	Surirella biseriata biseriata	1835	Breb. & Godey
SU006A	Surirella delicatissima delicatissima	1864	Lewis
SU010A	Surirella robusta robusta	1840	Ehrenb.
SU9999	Surirella sp.		
SY001A	Synedra ulna ulna	1836	(Nitzsch) Ehrenb.
SY002A	Synedra rumpens rumpens	1844	Kutz.
SY003A	Synedra acus acus	1844	Kutz.
SY010A	Synedra minuscula	1881	Grun. in Van Heurck
SY043A	Synedra famelica	1844	Kutz.
TA001A	Tabellaria flocculosa flocculosa	1844	(Roth) Kutz.
TA001B	Tabellaria flocculosa flocculosa IIIp		Koppen
TA002A	Tabellaria fenestrata	1844	(Lyngb.) Kutz.
TA003A	Tabellaria binalis	1881	(Ehrenb.) Grun. in Van Heurck
TA004A	Tabellaria quadrisepitata	1952	Knudson
TA005A	Tabellaria kutzingiana		Lange-Bertalot
TE001A	Tetracyclus lacustris	1843	Ralfs
ZZZ991	Nitzschia austriaca		
ZZZ992	Achnanthes [cf. doenensis]		
ZZZ999	Gomphonema [angustatum/parvulum]		