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Preliminary Study of the Ordination and Classification of Macroinvertebrate Communities from Running Waters in Victoria, Australia

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Abstract

Data on undisturbed lotic macroinvertebrate communities were assembled from a number of studies carried out in Victoria over the past 15 years; species-level information for 40 sites on nine rivers was available. Ordination (DECORANA and semi-strong hybrid multidimensional scaling) and classification (flexible UPGMA and TWINSPAN) techniques were used to assess the similarity of community composition among the sites. Correlation of environmental variables with both ordinations indicated that factors related to altitude and substratum were the most obvious gradients; a conductivity gradient was also present. The classification analyses identified four groups of sites that matched the altitudinal trends evident in the ordinations; but these techniques did not emphasize the substratum gradient. TWINSPAN also identified six groups of taxa that were characteristic of particular altitudes or regions or were widespread across all sites. The distinctiveness of the patterns from this preliminary study indicates that it would be worthwhile extending these analyses to much larger data sets from Victorian rivers.

Introduction

Classification and ordination techniques are commonly used to summarize the distribution patterns of lotic macroinvertebrate communities. Few studies, however, have attempted such summaries over wide geographic regions; notable exceptions are the extensive surveys carried out in the UK (Moss *et al.* 1987; Wright *et al.* 1989; Rutt *et al.* 1990), in north-western North America (Corkum 1989), and in New Zealand (Quinn and Hickey 1990). In this paper we present an analysis of the patterns of variation in lotic macroinvertebrate communities for the Australian state of Victoria, where a number of investigations have been conducted over the past 15 years. By analysing the available data as a single body of information, we hoped to determine the main aspects of community variation of such stream invertebrates.

It must be stressed that this study is a preliminary attempt to analyse community patterns for these biota in Victoria. The data available, although derived from widely scattered sites across the state, are not fully representative of the lotic habitats present in this region; for instance data are available for only one of the numerous northward flowing tributaries of the Murray River, and generally few data are available for the drier parts of the state. This situation results from the fact that the data had initially been gathered for a variety of purposes and that none of the rivers had been sampled specifically with a study such as this in mind.

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In addition, a particular concern was to use only data from sites that were known to be undisturbed (thus limiting the number of sites available) because the principal goal was to analyse natural patterns of community variation rather than those influenced by anthropogenic disruptions of the habitat. Although it was generally simple to establish whether upland sites had been disturbed (and could thus be excluded), it was more difficult to judge the degree of disturbance of lowland sites; as these were in cleared land, it was likely that all had suffered disturbances of one kind or another. Eventually, it was decided to include those lowland sites for which there was no evidence of disturbance other than that associated with clearing of the land; to do otherwise would have resulted in no lowland sites at all being available.

Thus, the aim of this paper is to present ordination and classification analyses of such baseline data. The patterns of community variation that are evident from these analyses are then associated with physico-chemical information to elucidate underlying environmental gradients. Detailed biological and environmental interpretations for particular river systems are not provided because these were usually provided in the original studies. The focus here is on the broad scale patterns of variation.

Methods

Data

Before data were accepted for analysis, two criteria had to be met in addition to the requirement that the sites were undisturbed. First, it was necessary that the taxonomic discrimination achieved by the various investigators was comparable and as near as possible to the species level for the major faunal groups. In Victoria, this last requirement has been achieved only by studies undertaken in the last 10–12 years. Second, it was important that each site had been sampled in at least two seasons (such as winter and summer) to lessen the chances of taxa being missed and unrepresentative data being included.

We assembled a composite data set (Table 1) from macroinvertebrate surveys carried out by the Museum of Victoria (MV) (Marchant *et al.* 1984, 1985), the Rural Water Corporation of Victoria (RWC) (Morley *et al.* 1989), and the Environment Protection Authority of Victoria (EPA) (Pettigrove 1989; Metzeling 1990*a*, 1990*b*; Metzeling *et al.* 1993; Chessman and Robinson, unpublished data). Quantitative data from a total of 40 sites on nine river systems in Victoria were available (Fig. 1, Appendix 1). Samples had been taken with Surber, Hess, air-lift and kick samplers (mesh sizes of 150–350 μm). The number of occasions on which each site had been sampled varied (Table 1), but all had been sampled at least in summer and winter (and often in other seasons) and usually for more than one year. The number of replicate samples at a particular site on a given date always exceeded five, which is the minimum number recommended by Marchant (1990*a*) for undertaking ordination or classification. Although the different sampling techniques will not give identical data at a given site, our experience suggests that any differences will be minor and will mostly be confined to rare taxa that have little impact on ordination or classification analyses (Gauch 1982).

Records were present for 651 taxa, which were identified mostly at the species or genus level. Exceptions were representatives of Oligochaeta, Tricladida and Hydracarina, which had usually not been identified to species in the various studies; in the data set, each of these groups was considered as a single taxon. In addition, taxa consisting solely of immature specimens were removed from the data set, and adult and larval Elmidae were treated as separate taxa. Because various groups were not identified to species level, the total number of species at a site (Table 1) was undoubtedly underestimated.

Because many of the taxa had not been described formally when the original studies took place, voucher systems were set up by the various investigators to simplify identification. We matched the names of the taxa in these differing systems of nomenclature, using available taxonomic information. However, taxonomic knowledge of many groups of lotic invertebrates increased markedly during the years over which the studies were conducted. Closely related species inevitably created problems; if they had not been reliably discriminated in all studies, then we lumped them into single genera. Despite this conservative approach, it seems likely that taxonomic inaccuracies were still present in the final data set.

Table 1. Summary statistics for the combined data set
Further details are given in Appendix I

Site	Number of species	Mean density of individuals (thousands per 0·1 m^2)	Number of sampling occasions
LLT1	137	1·1	12
LLT2	86	0·41	11
LLT11	84	2·1	6
LLT12	64	4·6	6
ULT1	81	0·21	6
ULT4	85	0·46	6
ULT5	74	0·38	6
ULT6	109	0·51	6
ULT12	109	0·53	6
ULT15	122	1·2	6
ULT28	98	0·37	6
ULT33	128	1·2	6
ULT35	91	0·81	6
ULT39	72	0·46	6
ULT41	119	1·1	6
ULT43	76	0·74	6
ULT52	105	0·77	6
ULT53	121	0·75	6
ULT55	83	0·40	6
ULT57	96	1·5	6
ULT60	126	2·0	6
YAR01	190	1·1	7
YAR02	139	0·89	9
YAR03	122	0·21	7
ELL01	145	2·1	3
BAT02	101	0·62	3
BAU03	138	1·3	3
WY04	116	1·1	3
EY05	124	1·1	3
FT06	168	2·3	3
BIG07	145	1·3	3
STI02	127	1·2	7
STI07	106	0·77	4
STI08	91	0·63	4
STI09	89	0·82	4
STI10	100	1·1	4
STI11	130	1·1	5
DCM07	108	1·5	7
WER05	121	1·1	7
WIM01	88	0·30	9

Ordination

Two ordination techniques were used: detrended correspondence analysis (DECORANA or DCA) and semi-strong hybrid multidimensional scaling (SSH). Programs for both techniques are contained within the PATN software package (Belbin 1993). SSH is currently considered to be the most robust ordination method available and has been described in detail elsewhere (Faith *et al.* 1987; Belbin 1993). It is particularly able to cope with the typical situation in which the responses of taxa to underlying gradients are unimodal, noisy and skewed. DCA (unlike SSH) has been widely used with benthic invertebrate data. It has been included here to provide a comparison with a familiar technique, although it is known to distort community patterns in

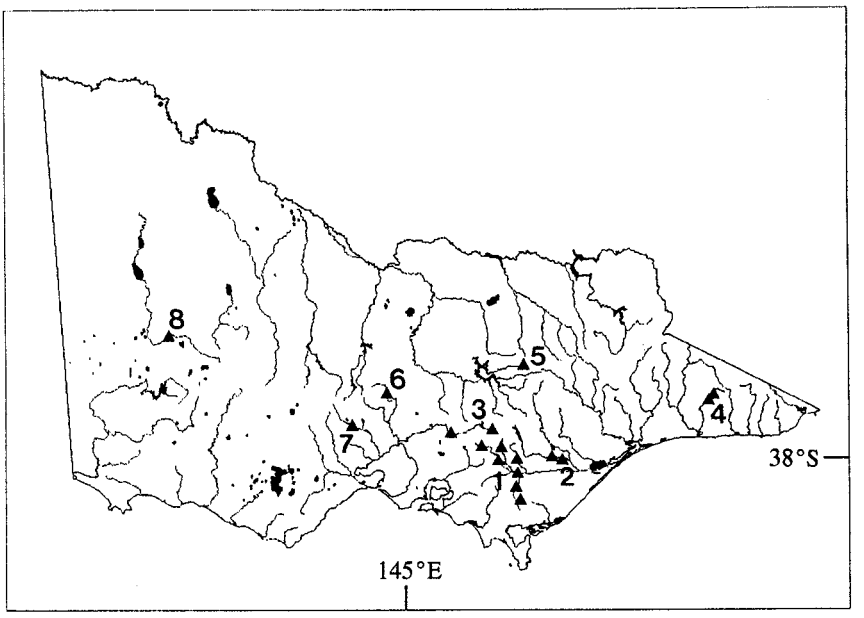

Fig. 1. Location of the study sites. In most cases, a single symbol encompasses a number of actual sampling sites. 1, La Trobe R.; 2, Thomson R.; 3, Yarra R.; 4, Brodribb R.; 5, Upper Delatite R. and Howqua R.; 6, Maribyrnong R.; 7, Werribee R.; 8, Wimmera R.

data sets with long underlying gradients (Minchin 1987). An important difference between the two techniques is that the number of dimensions for an SSH ordination must be specified before an analysis. Three dimensions were used in this study; this procedure is justified below. The Bray–Curtis association measure was used in all SSH ordinations; otherwise, default values were adopted.

All abundance values were converted to a common unit (number of individuals per $0{\cdot}1\ m^2$) and transformed to $\log(x+1)$ before analysis. Two data sets were constructed: DS1, in which samples taken on different occasions were kept separate (a total of 232 samples), and DS2, in which all data from a site were amalgamated to give a single sample (a total of 40 samples). For DS1, taxa that occurred in two samples or fewer were eliminated (giving a data set with 437 taxa) in order to reduce the taxa to a number (<500) that could be handled by DCA. Such a reduction was not required for SSH of this data set, and all 651 taxa were used. For DS2, taxa that occurred at only one site were eliminated to give a total of 471 taxa for analysis by both DCA and SSH. This procedure resulted in a decrease of $0{\cdot}1\%$ to 1% in total numbers at each site (except at Site WIM01, where the decrease was 15%), indicating that the eliminated taxa were rare and thus ought not to contribute greatly to the distinctiveness of a site (Site WIM01 remained distinctive, as shown below). The significance of the SSH ordination of DS2 was tested by using a Monte Carlo procedure: 100 simulations of the randomized data set were performed. This was a lengthy process for DS2 and thus was not attempted for the much larger DS1. Unfortunately, no software was available for similar Monte Carlo testing of the DCA ordinations.

In order to associate ordination patterns with environmental information, data (Table 2) on the following environmental variables were obtained from the reports of the original investigations: altitude (*Alt*), surrounding vegetation (*Veg*, as a ranked variable), stream bed substratum (*Sub*, as a ranked variable), mean current velocity (*Vel*), mean water temperature (*Temp*), annual water temperature range (*TempR*), mean pH (pH), mean electrical conductivity (EC), and mean dissolved oxygen (DO). These data were correlated with the DS2 ordinations only (insufficient data were available for DS1) by using the PCC (principal axis correlation) routine in PATN. This procedure calculates a vector of maximum linear correlation for each environmental variable in the reduced dimensional space (in this case, three dimensions) of the SSH and DCA ordinations. PCC also specifies the direction taken by a vector, which can then be plotted to depict an

Table 2. Environmental data for the 40 sites

Abbreviations are explained in the Methods (Ordination) section. Mean values are shown except for *Veg* and *Sub*, which are ranked variables. *Veg*: 1, agricultural land; 2, forest. *Sub*: 0, fine (sand or mud); 1, medium (mixture of sand, gravel and cobbles); 2, coarse (gravel, cobbles and boulders). EC was recorded at 25°C

Site	*Alt* (m)	*Veg*	*Sub*	*Vel* ($m\ s^{-1}$)	*Temp* (°C)	*TempR* (°C)	pH	EC ($mS\ m^{-1}$)	DO ($mg\ L^{-1}$)
LLT1	80	1	0	0·56	13·8	12·6	6·8	8·5	8·7
LLT2	50	1	0	0·67	13·7	12·6	6·7	10·3	9·1
LLT11	40	1	0	0·34	14·3	16·8	7·3	4·3	8·9
LLT12	20	1	0	0·33	15·3	17·0	7·3	5·1	8·9
ULT1	360	2	0	0·34	10·8	6·0	6·6	6·3	9·4
ULT4	480	2	0	0·30	8·9	8·7	7·3	4·4	9·8
ULT5	270	2	0	0·36	10·6	9·1	6·9	5·4	9·9
ULT6	400	2	2	0·58	8·9	6·5	7·1	6·2	8·8
ULT12	740	2	2	0·81	8·2	9·9	6·8	3·8	9·8
ULT15	150	2	2	0·47	11·4	10·0	7·0	5·6	10·1
ULT28	930	2	1	0·38	6·7	10·2	7·2	3·5	9·3
ULT33	180	2	2	0·62	10·6	7·1	6·9	4·7	9·1
ULT35	55	1	1	0·40	13·5	10·9	7·1	7·3	9·4
ULT39	170	2	0	0·25	13·3	10·0	6·8	23·2	8·9
ULT41	160	1	2	0·31	12·7	11·4	7·7	17·6	9·3
ULT43	60	1	0	0·25	14·0	12·2	7·9	21·2	9·4
ULT52	360	2	2	0·53	8·8	8·5	7·6	3·0	9·4
ULT53	240	2	1	0·45	10·3	11·0	7·1	6·4	9·4
ULT55	190	2	0	0·24	11·7	10·6	7·1	4·7	9·8
ULT57	60	1	2	0·49	14·4	12·8	7·1	11·2	8·5
ULT60	240	2	2	0·23	11·1	7·1	6·9	20·7	9·2
YAR01	440	2	2	0·70	9·6	6·9	6·9	2·3	11·2
YAR02	110	1	2	0·50	14·5	12·0	6·7	6·9	9·9
YAR03	110	1	0	0·13	16·4	11·4	6·7	7·0	9·5
ELL01	280	2	2	0·41	10·8	8·4	6·5	5·0	10·2
BAT02	500	2	2	0·44	10·1	7·2	6·3	4·1	10·2
BAU03	260	2	1	0·46	10·5	9·9	6·5	6·2	10·1
WY04	360	2	2	0·36	10·5	6·6	6·4	6·1	10·1
EY05	360	2	2	0·32	10·5	5·9	6·4	6·1	10·1
FT06	220	2	2	0·48	11·0	9·9	6·5	7·1	10·3
BIG07	310	2	1	0·62	10·8	7·0	6·7	6·6	10·6
STI02	1240	2	2	0·70	6·0	7·8	6·7	1·1	10·6
STI07	1090	2	2	0·53	7·7	8·5	7·0	1·2	11·1
STI08	1400	2	2	0·45	6·2	6·5	6·8	1·0	10·9
STI09	1130	2	2	0·59	6·9	5·0	7·3	2·3	11·1
STI10	1090	2	2	0·61	7·6	6·5	7·2	1·1	10·9
STI11	800	2	2	0·55	9·3	8·0	7·2	1·2	10·6
DCM07	380	1	2	0·60	11·0	10·0	7·6	112·7	9·5
WER05	130	1	2	0·45	13·4	6·1	7·5	44·4	10·2
WIM01	130	1	0	0·00	16·0	9·5	8·2	176·5	6·5

environmental trend on the ordination itself (called a biplot). The significance levels of the correlation coefficients were tested by Monte Carlo procedures; 1000 simulations of randomized environmental data were used in all analyses.

Classification

Classification techniques were applied to DS2 only; DS1 was considered too large for easy presentation of classification results. Two techniques were used: flexible unweighted pair-group arithmetic averaging (flexible UPGMA) of the Bray–Curtis association measure (an agglomerative

hierarchical technique), and two-way indicator species analysis (TWINSPAN). Programs for these routines (ASO, FUSE, TWIN) are available in PATN (Belbin 1993). Flexible UPGMA was applied to the full set (471 taxa) of log-transformed data, whereas TWINSPAN was applied to a subset because there were too many taxa in the full data set to handle; for TWINSPAN, taxa with mean abundances across all sites of <0·25 individuals per 0·1 m^2 were removed, leaving 234 taxa. Untransformed abundances were expressed as three levels of abundance (cut levels) on the following scale: >0, >10 or >100 individuals per 0·1 m^2.

Results

Ordination of DS1 (Sites and Dates Separate)

Ordinations of DS1 by DCA (437 taxa) and SSH (651 taxa) revealed broadly similar patterns (Fig. 2). DCA ordination tended to group the samples into site groups (Fig. 2*A*) so that samples from the same river system clustered together in the ordination space, but these site groups were themselves arranged so that a strong altitudinal gradient was evident on the first axis (Fig. 2*B*). The second axis distinguished samples from the Yarra and the rivers to the west of Melbourne from those taken to the east of Melbourne (the Gippsland region); samples from the upper Delatite fell in an intermediate position. It is possible that the strong clustering of samples from the same river system in this DCA ordination is somewhat of an artefact resulting from distortions introduced by this ordination technique. Minchin (1987) showed that distortions to the underlying community pattern occurred when DCA axes exceeded 5–6 standard deviation (s.d.) units in length; the first axis of this DCA ordination is 4·5 s.d. units.

SSH (Fig. 2*C*) showed a more continuous spread of the samples in ordination space, with less obvious clumping of the data from single river systems. An altitudinal gradient was still evident (Fig. 2*D*); in this case, Axes 2 and 3 were plotted because they gave the clearest view of the gradient. (With SSH the position of the axes is arbitrary (Belbin 1993) and maximum variance does not necessarily occur on the first axis.) The stress value (0·22) was high indicating a poor fit between the original association measures and the final SSH configuration (Belbin 1993). However, the altitudinal gradient was clear and there seemed to be little point in increasing the number of axes (as a means of lowering the stress) when there was no indication from DCA that an interpretable pattern existed in more than two dimensions.

In neither of these ordinations was there any indication of the seasonal changes in the communities that were demonstrated in the original studies (e.g. Marchant 1988). This was probably because the studies were conducted during different periods (see Appendix 1) with different frequencies of sampling; thus, there was no synchrony of sampling among the various studies. If such synchrony had occurred, a stronger seasonal signal might have been evident in the ordinations.

Ordination of DS2 (Sites Only)

The ordinations of DS2 (Fig. 3) produced patterns that were similar to those obtained from ordinations of DS1. DCA appeared to impose more clumping on sites from the same river system than did SSH (as in Fig. 2), but both techniques clearly indicated that a strong altitudinal gradient was present (Figs. 3*B* and 3*D*). DCA (Fig. 3*A*) distinguished the Yarra sites and those west of Melbourne from the Gippsland sites on Axis 2. Such a trend was not obvious in SSH (Fig. 3*C*) and may again be something of an artefact with DCA. Axis 3 of the DCA added little to the pattern on the first two axes and is not considered further.

The stress value for the SSH ordination (0·19) is in the range (0·15–0·2) for which Belbin (1993) urges caution in interpretation of the result. Adding dimensions to the solution decreased the stress (to 0·09–0·14 for four to six dimensions) but added noise to the ordination. A Monte Carlo simulation of DS2 demonstrated that the lowest stress

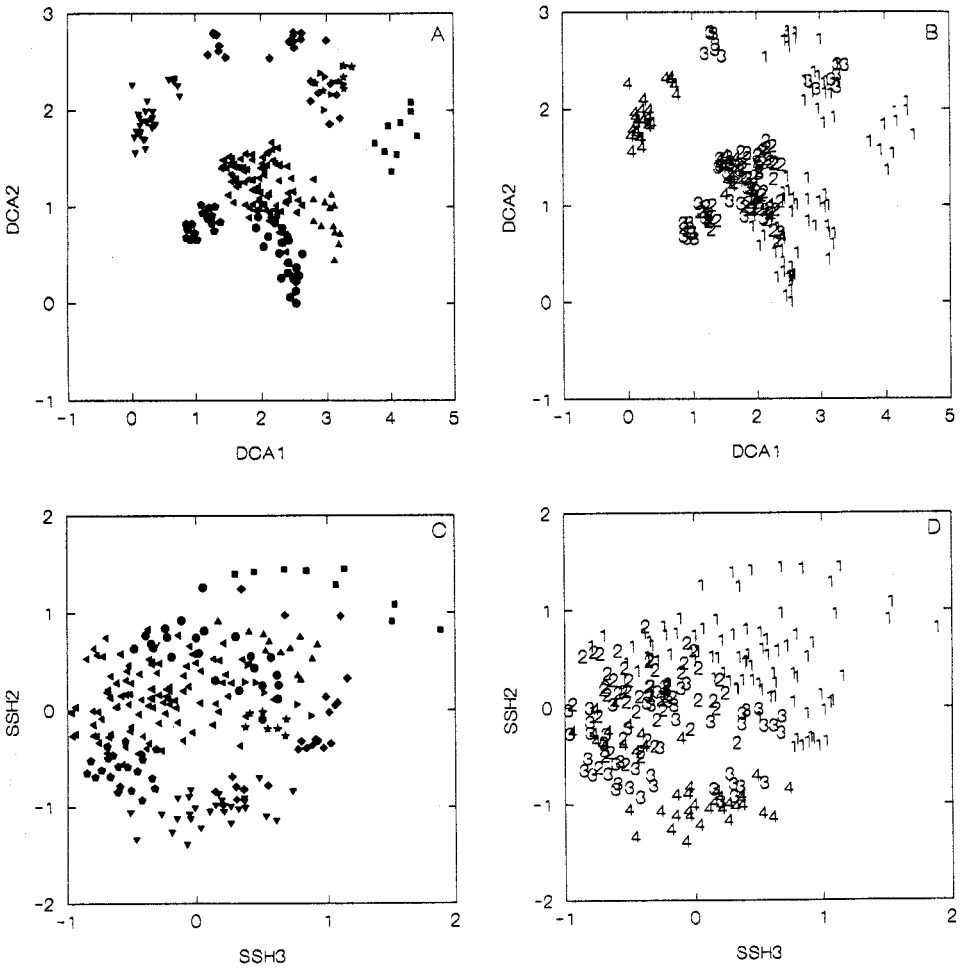

Fig. 2. DCA and SSH ordinations of DS1 (232 samples, sites and dates separate). (*A*) DCA Axis 2 versus Axis 1 (site symbols: ▼, upper Delatite and Howqua; ⬟, Brodribb; ◀, upper La Trobe; ●, lower La Trobe; ▲, Thomson; ◆, Yarra; ▶, Werribee; ★, Deep Creek; ■, Wimmera); (*B*) DCA Axis 2 versus Axis 1 with altitude superimposed (altitude codes: 1, <150 m; 2, 150–300 m; 3, 300–600 m, 4, >600 m); (*C*) SSH Axis 2 versus Axis 3 (site symbols as for *A*); (*D*) SSH Axis 2 versus Axis 3 with altitude superimposed (altitude codes as for *B*). For DCA plots, axis scales are in s.d. units and eigenvalues are 0·50 (Axis 1) and 0·27 (Axis 2). For SSH plots, stress is 0·22.

for a three-dimensional solution from randomized data was 0·28. Thus, on the basis of statistical significance alone, a three dimensional solution seems justified.

To enable further interpretation, the environmental data (Table 2) were correlated with the two ordinations of DS2 (Table 3). As nine variables were correlated with each ordination, it is probably wise to consider only those correlations with $P < 0·006$ (0·05/9) as significant. Thus, *Vel* was not significantly correlated with either ordination, and pH was significant for the SSH only. *Alt*, *Temp* and DO clearly had the highest correlations ($r > 0·8$); these variables are interrelated and are merely different ways of expressing an altitudinal gradient. The two ranked variables (*Sub* and *Veg*) also gave high r values on both ordinations (0·67–0·86). Variation in *Veg* is another reflection of changes in altitude: high sites were generally in forested areas. However, as *Veg* can take only two

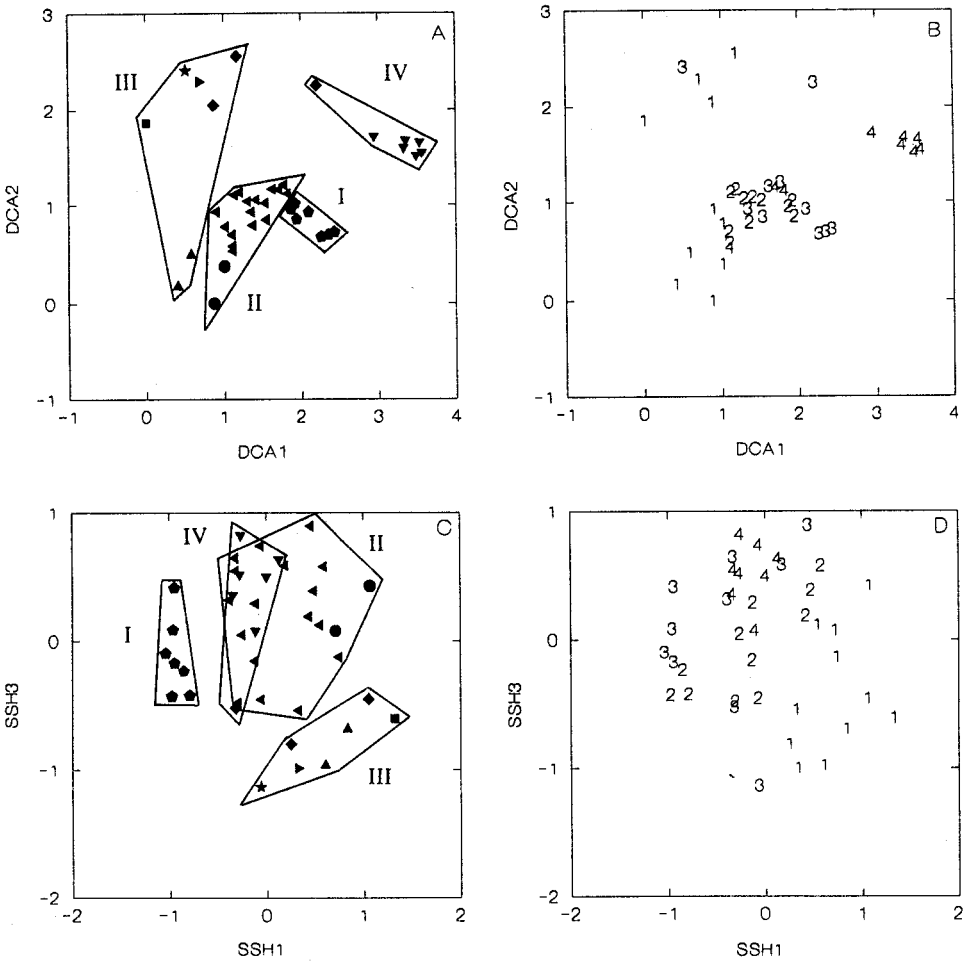

Fig. 3. DCA and SSH ordinations of DS2 (40 samples, one for each site). (*A*) DCA Axis 2 versus Axis 1 (site symbols as for Fig. 2*A*); (*B*) DCA Axis 2 versus Axis 1 with altitude superimposed (altitude codes as for Fig. 2*B*); (*C*) SSH Axis 3 versus Axis 1 (site symbols as for Fig. 2*A*); (*D*) SSH Axis 3 versus Axis 1 with altitude superimposed (altitude codes as for Fig. 2*B*). For DCA plots, axis scales are in s.d. units and eigenvalues are 0·47 (Axis 1) and 0·26 (Axis 2). For SSH plots, stress is 0·19. Polygons I–IV indicate site groups derived from the flexible UPGMA of DS2.

values, it is a coarse measure of trends in vegetational abundance; this probably contributes to its high correlations with the ordinations. *Sub* is also a coarse measure (only three values, Table 2), but the sizes of its correlations do reflect the reasonably clear trends in stream-bed substratum (see below).

The remaining variables had lower correlations or did not have consistently high values on both ordinations. In particular, the correlations for *Vel*, which were low, should be treated with caution. Water velocity is likely to vary more rapidly and to a greater extent within a short period (e.g. months) than are any of the other variables. Thus, mean water velocities are probably not as representative of trends among sites as are mean values for the other variables.

The underlying environmental gradients are best displayed on biplots (Fig. 4). For the DCA ordination of DS2, vectors for *Alt*, *Vel* and DO point in almost the same direction (Fig. 4*A*), whereas the vector for *Temp* points in the opposite direction. Taken together,

Table 3. Correlation coefficients of the environmental variables with the DCA and SSH ordinations of DS2

P values were derived from 1000 random simulations of each variable

Variable	DCA *r*	*P*	SSH *r*	*P*
Alt	0·88	<0·001	0·82	<0·001
Veg	0·71	<0·001	0·86	<0·001
Sub	0·67	<0·001	0·78	<0·001
Vel	0·47	0·032	0·56	0·006
Temp	0·84	<0·001	0·86	<0·001
TempR	0·83	<0·001	0·68	<0·001
pH	0·50	0·013	0·56	0·004
EC	0·75	<0·001	0·55	<0·001
DO	0·80	<0·001	0·85	<0·001

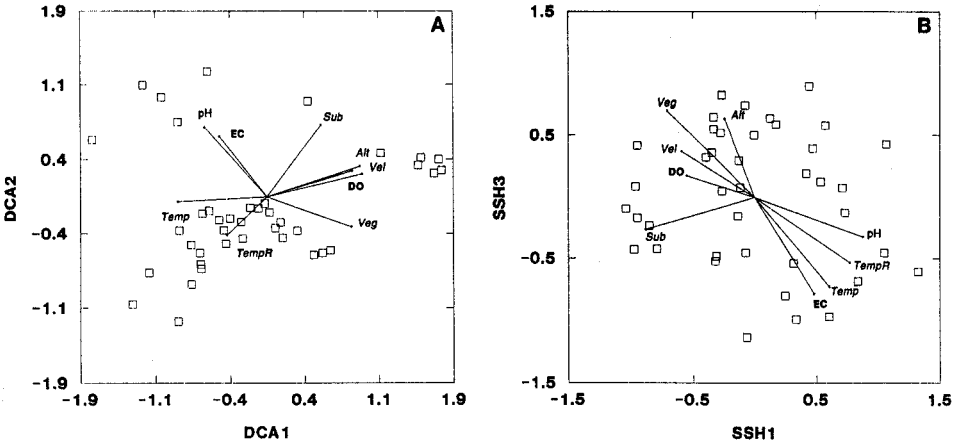

Fig. 4. Biplots for the (*A*) DCA and (*B*) SSH ordinations of DS2. The DCA ordination was centred before the environmental vectors were superimposed; this was not required for SSH (see Fig. 3*C*). The vectors are labelled with abbreviated names explained in the Methods (Ordination) section.

these four vectors can be considered as a general altitudinal gradient, as noted above. The direction of the *Sub* vector reflects the trend for sites with fine substratum to occur at the bottom left of Fig. 4*A*. The vectors for EC and pH point at the sites to the west of Melbourne, which had higher values for these variables (especially EC, Table 2).

For the SSH ordination (Fig. 4*B*), the vectors appear to show only two main gradients: an altitudinal gradient comprising eight of the nine vectors and, more or less at right angles to this, a substratum gradient represented by *Sub*. Sites with fine substratum occur on the right of Axis 1 (Fig. 4*B*), and those with coarse substratum occur on the left. In this SSH ordination, pH and EC are associated with the altitudinal gradient more than they are in the DCA configuration. Axis 2 of the SSH is not shown but largely repeats the altitudinal gradient.

Classification of DS2 (Sites Only)

The dendrogram resulting from the application of flexible UPGMA to this data set is too large for display here. However, four groups (I–IV) emerged from this analysis, and these have been superimposed on the ordination diagrams (Fig. 3*A* and 3*C*). The four groups are more or less distinct from one another when plotted on the first two axes of the DCA ordination. The groups themselves represent either geographic distinctions—Group I is composed exclusively of sites from the Brodribb, whereas Group II comprises those

from the upper and lower La Trobe—or altitudinal differences—Group IV includes sites from high altitudes (the upper Delatite, Howqua and the highest site on the Yarra) whereas Group III contains most of the lowland sites.

The four groups appear less distinct when plotted on Axes 1 and 3 of the SSH ordination, owing to the overlap of Groups II and IV. However, this overlap disappears on Axis 2: here, the high-altitude group (IV) is clearly separated from Group II. This pattern reinforces the conclusion from the correlation analysis, which indicated that Axis 2 of the SSH also reflected an altitudinal gradient.

Flexible UPGMA of DS2 did not produce major site groupings that reflected differences in substratum. Sites with fine sediments, however, formed subgroups within Groups II and III: sandy or muddy sites were generally grouped together, as were those with stony substrata. Unfortunately, these subgroups, though evident, were not sufficiently distinct to be considered as major groups. Classification is thus not always the most appropriate analytical technique; it seeks clear breaks in the data, which may not be present, and ignores trends or gradients. Trends and gradients are more clearly revealed by ordination, which emphasizes the continuous nature of variation in the data.

The TWINSPAN analysis of DS2 (Table 4) also produced four groups of sites (A–D). Group A was identical to Group I, while Group B was very similar to Group II except for the inclusion of the highest site on the Yarra (YAR01) and one of the Thomson sites (LLT11). Groups C and D were thus equivalent to groups III and IV respectively, except for the absence of these two sites. Subgroups of sites with differing substrata were not as evident with TWINSPAN as they were with flexible UPGMA; Belbin and McDonald (1993) have examined in detail such differences between the two techniques.

Six groups of taxa (1–6) were also evident from TWINSPAN (Table 4), among the 90 most common taxa. Groups 1 and 2 comprised taxa that were often rare or absent at the high-altitude sites on the Delatite and Howqua (Site Group D) and that were most abundant and frequent in central and eastern Gippsland (the La Trobe, Thomson and Brodribb sites in Site Groups A and B). Group 3 contained species generally absent or uncommon at the Brodribb sites. Taxa in Group 4 were commonly found at all sites; it is perhaps not suprising that a number of the taxa in this group were broadly defined (genera or higher taxa rather than species). Finally, Groups 5 and 6 contained taxa that were generally not abundant or frequent at lowland sites.

Discussion

It is clear from the ordination and classification analyses that the changes shown by macroinvertebrate communities in Victorian streams and rivers are largely related to changes in altitude and in those variables closely correlated with this (water temperature and dissolved oxygen). Compositional changes with altitude have been widely reported for stream macroinvertebrates (e.g. Hynes 1970; Corkum 1989; Rundle *et al.* 1993). It is, of course, improbable that these communities are responding to altitude directly; more likely, they are responding to a host of environmental factors (in addition to dissolved oxygen and water temperature) that vary with altitude (e.g. discharge, flow patterns, nutrient loads, inputs of organic matter). Unfortunately, detailed measurements of such factors were unavailable for analysis here. In addition, attempts to relate altitudinal gradients in species composition to variation in complex hydraulic variables (as suggested by Statzner *et al.* 1988) have not been successful in Victoria; for instance, no correlation was shown between changes in Froude numbers (a measure of turbulence) and changes in macroinvertebrate communities at cobble sites in the upper La Trobe (Marchant 1988).

Variations in substratum also play an important role in the present data, with communities on rocky river beds generally being distinguished from those on sandy or silty beds. This was more readily shown by the ordinations than by the classifications. Changes in substratum and position along a river (a feature related to altitude) were major factors

Table 4. Ordered table of species (90 most common taxa) and sites (columns) derived from TWINSPAN

Numbers refer to the three cut levels used in the analysis and represent three logarithmic levels of abundance. Site groups have been labelled with the names or regions of the main river systems represented in the group. MV and LTCS, Museum of Victoria voucher numbers; RWC, Rural Water Corporation of Victoria voucher numbers; other code numbers refer to nomenclature in identification keys (see Appendix 2)

Taxon	Site group A (Brodribb)	B (La Trobe)	C (lowland)	D (Delatite)
Group 1				
Ulmerophlebia pipinna	-112112	-----1-1--11---11---1	1-1--1	------
Neboissophlebia hamulata	1--1121	1-1--1--1-121111111-1	--1-11	------
Austrophlebioides sp. A3	2113223	1-12232222-11-2-11112	------	------
Baetis sp. MV2	2221212	----1--111------11---	------	1-----
Dinotoperla eucumbene	111-111	--11111111-1---------	------	------
Austrocercella/Austrocercoides spp.	1111111	11111-2-1--1---12--12	1-1---	------
Simsonia sp. L3E	---1112	---111-211-------1--1	1-----	------
Notriolus quadriplagiatus	1221111	----1-----1-1111-----	----11	------
Austrolimnius sp. L13E	1112233	11211-1222---1--2-111	111---	------
Tipulidae sp. MV4	1221122	-------11-11--------1	------	------
Nilotanypus sp. MV108E	1111121	1-1--1-11--11-1--1-1-	------	------
Polypedilum oresitrophum	1221112	----------	1-11-1	-1----
Stempellina sp. MV58E	-111122	1--111-111-11--11-112	---1--	------
Bezzia sp. RWC5	1112112	-1-----1--11---11---2	1--111	------
Hydrobiosella spp.	1111111	---11-11-111---------	--1---	-1----
Ecnomina Group E spp.	1111--1	-----1-111111-1---11-	------	------
Notalina bifaria	-112222	-----2-111111-1-1-1-2	------	------
Dinotoperla fontana	----111	-1---1-11111---11-1-1	-1----	1-----
Riekoperla alpina group	11--11-	11111-2111----1---1-1	------	------
Trinotoperla yeoi	---1111	111111-11-21----1---1	1---1-	-1----
Archichauliodes sp.	-11-111	----11111111----1--1-	1-2-1-	1-----
Aphroteniella tenuicornis	-112122	1111-1-21122111---11-	-1--11	11----
Podochlus sp. MV112E	1111111	1111111111-11-111-1-1	------	------
Parakiefferiella spp.	-222122	-11111111212122121123	132-11	111---
Tanytarsus spp.	2333132	111122-11212132223122	121111	-1111-
Asmicridea sp. 1	-1-1111	---111-111-1111-1--21	-1----	------
Aphilorheithrus sp.	11-1111	11111111-1-11--11-1-1	------	1-----
Austrheithrus sp.	-111-11	1--111-11-11---111--1	------	------
Group 2				
Potamopyrgus spp.	-------	1-111--1-11----221--2	1-2---	------
Nousia sp. MV1	-------	11111-1-112----1--11-	2---11	------
Baetis sp. MV3/MV1	---1111	1212122221-1111121112	------	------
Pentaneura sp. MV7E	-1-1111	111-111111--12111-111	-1----	------
Procladius spp.	------1	1----111-1-1121111112	-1----	------
Zavreliella sp. MV54E	-21----	--1112-122-1------1-2	------	-1----
Polypedilum tonnoiri	---1-21	1121121111-1121123123	111212	------
Cladopelma sp. LTCS12	-------	--1-111111-121111--1-	----1-	-1----
Harnischia sp. MV68E	---1---	--1-1-1--1-11111-1-11	-1--11	------
Parachironomus sp. LTCS2	-------	-11--1-111-11-21-1221	------	------
Corynoneura sp. MV63E	---1-1-	-----1-2-1-2211---211	------	------
Cricotopus spp.	111-112	1211121211-2122222123	1211--	------
Bezzia sp. MV2	---1111	1111111111-111-12-112	------	------
Ferrissia tasmanica	-------	11-1---1--11--1---111	3-31-1	-----1
Corbiculina australis	-------	111-11---11111111111-	311111	1-----
Austrophlebioides pusillus	-------	-----2-11121111131-12	----21	-----2

Table 4. *(Continued)*

Taxon	Site group A (Brodribb)	B (La Trobe)	C (lowland)	D (Delatite)
Tasmanocoenis spp.	---2121	11-112121111131121122	132221	11----
Dinotoperla serricauda/thwaitesi	--1----	11-111------1---1--1-	212---	1-----
Empididae sp. MV3	-------	-1--1---1-111211-1121	121-11	--1---
Group 3				
Coloburiscoides spp.	-------	1-11111111111-1--1---	-1--1-	--11--
Austrosimulium furiosum	---1-12	1-1112121111111121112	212-21	11-111
Ablabesmyia spp.	-1---1-	1121111111-2111212112	1111--	11-11-
Orthocladiinae sp. 'grape th'	-------	---1-1----1111----1--	122-21	111--1
Stictocladius uniserialis	-------	2221222222223212222221	-11-11	221112
Empididae sp. MV2	-------	-11111111111--1111112	1-1-1-	111--1
Byrrocryptus sp.	-------	11-121-1111----11-1-1	-----1	1-1-11
Austrosimulium victoriae	---1-11	-1-11212111---1-211-2	------	111--1
Edwardsina polymorpha	1---1--	-1-1111211-11--------	------	1-1---
Group 4				
Tricladida	--11111	-11-1--1--111---11-1-	211111	1-1---
Oligochaeta	2222222	223223232323333233233	333232	333233
Hydracarina	1112122	111122121222121111122	222121	211111
Illiesoperla spp.	1111111	1--11-111-1----111-11	1-1-1-	-1-111
Tipulidae sp. MV3	1111111	11111111111111111-111	----1-	11--1-
Tipulidae sp. MV1	11-1111	211111111111111211111	-1---1	111111
Tipulidae sp. MV10	1121111	1111111111111-1111111	----11	211111
Riethia stictoptera	2322232	112113221223111121222	1-1111	3111-1
Rheotanytarsus spp.	1231212	111112121221112131133	222-21	111-21
Taschorema complex	1111112	-11111111111111111-11	2-1-11	211-11
Austrolimnius Group A spp.	2222333	1323222322121122222222	2-2-11	122222
Agapetus spp.	1112222	-11221122221---111111	2-1-21	221111
Smicrophylax spp.	---1212	----11111121--1---111	1-1-2-	2-----
Austroneurorthus sp.	1111111	11111---111---------1	------	1----1
Tamasia acuta	-112222	----11112121----1-1-1	----1-	11----
Group 5				
Nousia sp. MV2	1222212	1111111111-2112121111	11----	122221
Stenoperla kuna	11-1111	111111111111--1-1---1	------	1111-1
Acruroperla atra	-111111	-1--1-11111-------1-1	----11	11---2
Scirtidae	2222222	2122211212221-1111212	2----1	232212
Sclerocyphon maculatus	-111122	1111111111-----11---2	----1-	1111-1
Thienemaniella trivittata	2222222	1111121111121112111112	212-11	122122
Austropentura victoria	---11--	11111-1111111-------1	-1----	111111
Apsilochorema spp.	111-111	111111-11111----1---1	1-1-1-	11111-
Podonomopsis sp. MV71E	2111112	-1-1112221-1--1-111-1	----1-	112111
Orthocladiinae sp. MV117E	2222221	11-11111-121------1--	------	121122
Group 6				
Pseudomoera fontana	1231-11	------1---2----------	----11	122332
Eusthenia venosa	211-1--	-1-11-1---1----------	------	-21111
Riekoperla tuberculata group	111-111	11-11111111-111--111-	--1-21	122222
Riekoperla rugosa group	1111112	-1111111111----11-111	----1-	122221
Austropsyche victoriana	2121111	1111-1---11---1--1---	----1-	122222
Conoesucus sp. MV1	-----11	---1-11--11---1111--2	------	211122
Conoesucus sp. MV10	---1-1-	11-111-111-----1-----	11----	222112
Alloecella grisea	211-211	---1111-111---1-----1	------	2-2132
Trinotoperla irrorata	-------	---11-1111----------	--1---	112211

influencing macroinvertebrate distribution in unpolluted British running waters (Wright *et al.* 1984). The major influence of substratum on benthic macroinvertebrate communities in flowing waters has long been appreciated (Hynes 1970).

Differences in conductivity play a minor (but detectable) role in the data sets, distinguishing sites in dry regions to the west of Melbourne from those in the wetter east. Additional sampling by Metzeling (1993) in the Maribyrnong River (west of Melbourne) upstream and downstream of the site in the present data sets (DCM07) showed that distinct invertebrate communities characterized these sites, which had naturally high conductivities. Thus, if the sites in the present data sets were more fully representative of Victorian running waters, particularly those in the drier regions, then conductivity might appear as a stronger gradient.

The environmental factors are consistent with those identified in the original studies from which the data sets were drawn. Marchant *et al.* (1985) and Marchant (1990*a*) showed that macroinvertebate communities in the upper La Trobe responded mostly to changes in substratum and altitude. Data from the lower La Trobe and Thomson sites have not been analysed previously in conjunction with data from higher altitudes; not suprisingly, the altitudinal gradient distinguishes macroinvertebrate communities at these lowland sites from those at the upland sites (see Fig. 3). Altitudinal gradients were also clearly evident in the original studies of the Yarra sites (Pettigrove 1989) and the Delatite and Howqua sites (Morley *et al.* 1989). The sites west of Melbourne consisted of single (undisturbed) sites from three separate rivers, and the composition of their macroinvertebrate fauna had been analysed only in relation to that at downstream disturbed sites (Metzeling 1990*a*, 1990*b*; Metzeling *et al.* 1993), which are not considered here. No previous analysis had been carried out on the Brodribb sites.

It is worth noting that essentially the same environmental factors or gradients were revealed by the two different ordination procedures, SSH and DCA. According to simulation studies by Faith *et al.* (1987) and Minchin (1987), the DCA procedure is liable to distort underlying community structure, especially when the length of an axis exceeds 5–6 s.d. units (see Figs 2 and 3); their simulations suggest that SSH is much less prone to such problems. The apparent robustness of ordination patterns in the present study perhaps indicates that the underlying gradients are particularly strong and are thus likely to be revealed no matter which technique is used. The clumping of sites from the same river system, noted previously in the DCA ordinations, is the only obvious difference between the outcomes of the two techniques. This phenomenon does not seem to interfere with the interpretation of the gradients.

As the analyses described here are preliminary, detailed discussion of the distribution of various taxa along the gradients is not justified. This is particularly the case with these data, in which various taxonomic compromises have had to be made in order to assemble the information in the first place. However, the distribution of certain taxa certainly conforms to general knowledge. Thus, the Plecoptera are confined to the higher altitude sites (Table 4): about half of the common Plecoptera occur in Groups 1 and 2, which are characteristic of Gippsland sites and have generally infrequent occurrences at low altitudes (Site Group C); the other common Plecoptera occur in Groups 5 and 6, which typify the high-altitude sites on the La Trobe, Delatite, Howqua and Brodribb. The ephemeropteran genus *Austrophlebioides* is common on rocks in stony upland streams (Peters and Campbell 1991) in south-eastern Australia. Table 4 indicates that two species in this genus are frequent at stony sites in the Brodribb and the upper La Trobe (Site Groups A and B respectively) but are not found commonly at lowland sites (Site Group C) or at sandy sites (the first three sites in Group B). Declines in populations of *Austrophlebioides* have been observed at sites disturbed by sedimentation (Doeg *et al.* 1987; Doeg and Milledge 1991). The bivalve *Corbiculina australis* (Group 2, Table 4) is often abundant in sandy rivers (Smith and Kershaw 1979), which are represented here by a number of the sites in Groups B and C.

The distinctive patterns of distribution shown by some of the species groups (Table 4) suggests that they may be useful as indicator groups of particular environmental conditions. Thus, Groups 5 and 6 include species (in addition to the Plecoptera mentioned above) that are commonly encountered at the higher-altitude rocky sites. Groups 1 and 2, on the other hand, comprise species that are found at more intermediate altitudes. Obviously, as taxonomic knowledge improves and larger data sets are analysed these types of indicator groups can be more closely specified.

The data and analyses presented in this paper are clearly limited. Nevertheless, the ordination and classification patterns are distinct even though the quantitative data on which they are based come from a variety of studies using different sampling techniques. Marchant (1990*a*) showed that ordinations and classifications of sites on the La Trobe River based on binary (presence/absence) data were indistinguishable from those based on quantitative abundances. It seems likely that the same will hold for the larger data set considered here, because the patterns evident from the analyses are probably a consequence of the large spatial scale of the study. Gauch (1982) concluded that most of the pattern in large-scale studies of diverse communities lies in the qualitative differences in species composition between sites. The detailed effects on the present ordinations of relying on binary data or reducing the degree of taxonomic discrimination will be dealt with elsewhere.

Given that the data used in these analyses come from only 40 sites on nine rivers, it is premature to attempt to construct a predictive model of the sort used in Great Britain (Wright *et al.* 1984); the preliminary predictive system in that study was based on 268 sites from 41 rivers. Nevertheless, the gradients underlying the distribution of the macroinvertebrate fauna in the present study are distinct, and this can only provide confidence in extending these sorts of analyses to much larger data sets from Victoria.

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Appendix 1. The 40 sites used in the multivariate analyses, grouped into regions

The years over which samples were taken and the organisations that took the samples are also shown. Grid references were obtained from the National Topographic Map Series 1:100 000

Site Description	Grid reference	Site code
Lower La Trobe sites (1979–1981, MV)		
La Trobe R. at Willow Grove Rd[A]	8121-262-839	LLT1
La Trobe R. at Moe–Willow Grove Rd[A]	8121-346-773	LLT2
Thomson sites (1980–1981, MV)		
Thomson R. at Rosedale–Heyfield Rd[A]	8222-806-956	LLT11
Thomson R. at Maffra–Rosedale Rd[A]	8221-894-929	LLT12
Upper La Trobe sites (1979–1980, MV)		
La Trobe R. at Powelltown–Noojee Rd	8022-950-077	ULT1
Ada R. at Ada River Rd	8022-005-106	ULT4
La Trobe R. west of Noojee	8022-016-066	ULT5
Loch R. north of Noojee	8022-093-166	ULT6
Toorongo R. south of Toorongo Rd	8122-178-174	ULT12
La Trobe R. at Hawthorn Bridge	8122-196-968	ULT15
Western Tanjil R. at Saxtons Rd	8122-294-161	ULT28
Eastern Tanjil R. at Tanjil Junction	8122-292-963	ULT33
Tanjil R. at Moe–Walhalla Rd	8121-357-783	ULT35
Little Morwell R. at Thorpdale–Mirboo North Rd	8121-286-525	ULT39
Middle Ck at Middle Ck Rd	8121-465-487	ULT41
Morwell R. at Driffield–Yinnar Rd	8121-415-595	ULT43
Western Tyers R. at Christmas Ck Rd	8122-343-042	ULT52
Middle Tyers R. above Tyers junction	8122-414-985	ULT53
Tyers R. at Moe–Walhalla Rd	8121-412-899	ULT55
Tyers R. at Yallourn North–Tyers Rd	8121-516-774	ULT57
Traralgon Ck at Traralgon Ck Rd	8221-576-475	ULT60
Yarra sites (1983–1988, EPA)		
Yarra R. upstream of Upper Yarra Dam	8122-178-233	YAR01
Yarra R. upstream of Woori Yallock	8022-708-187	YAR02
Yarra R. downstream of Woori Yallock	8022-706-184	YAR03
Brodribb sites (1985–1986, EPA)		
Ellery Ck at Goongerah	8623-522-655	ELL01
BA Ck top site	8623-546-614	BAT02
BA Ck upstream of mine	8623-500-605	BAU03
West Yabby Ck	8623-532-565	WY04
Ferntree Ck top site	8623-536-566	EY05
Ferntree Ck on Sardine Ck Rd	8623-490-569	FT06
Big R. on Big River track	8623-557-530	BIG07
Upper Delatite and Howqua sites (1985–1989, RWC)		
Lower Baldy Ck	8123-524-921	STI02
Falls Ck	8123-517-919	STI07
Dugout Ck	8223-568-911	STI08
'Howqua Gap' Ck	8123-546-879	STI09
Upper Delatite R.	8123-525-895	STI10
Delatite R. upstream of Mirimbah	8123-499-920	STI11
Sites west of Melbourne (1985–1988, EPA)		
Deep Ck (Maribyrnong R.) east of Romsey	7823-053-625	DCM07
Werribee R. upstream of Bacchus Marsh	7722-672-273	WER05
Wimmera R. upstream of Horsham	7324-104-380	WIM01

[A] At these sites, both main-channel and bank samples were available; only the main-channel samples were used in constructing the data sets.

Appendix 2. Systematic list of the 90 most common taxa (Table 4)

Species code numbers or letters are those used in the voucher collections of the Museum of Victoria (MV) or the Rural Water Corporation (RWC) or in the following keys: Marchant (1990*b*); Cranston (1994); Dean (1991); Glaister (1992)

Gastropoda
- Hydrobiidae
  - *Potamopyrgus* spp.
- Ancylidae
  - *Ferrissia tasmanica* (Tenison-Woods)

Bivalvia
- Corbiculidae
  - *Corbiculina australis* (Deshayes)

Tricladida

Oligochaeta

Hydracarina

Amphipoda
- Eusiridae
  - *Pseudomoera fontana* Sayce

Ephemeroptera
- Leptophlebiidae
  - *Ulmerophlebia pipinna* Suter
  - *Neboissophlebia hamulata* Dean
  - *Austrophlebioides pusillus* (Harker)
  - *Austrophlebioides* sp. A3
  - *Nousia* sp. MV1
  - *Nousia* sp. MV2
- Baetidae
  - *Baetis* sp. MV2
  - *Baetis* sp. MV3/MV1
- Caenidae
  - *Tasmanocoenis* spp.
- Coloburiscidae
  - *Coloburiscoides* spp.

Plecoptera
- Eustheniidae
  - *Stenoperla kuna* Theischinger
  - *Eusthenia venosa* (Tillyard)
- Austroperlidae
  - *Acruroperla atra* Samal
  - *Austropentura victoria* Illies
- Gripopterygidae
  - *Dinotoperla eucumbene* McLellan
  - *Dinotoperla serricauda/thwaitesi*
  - *Dinotoperla fontana* Kimmins
  - *Trinotoperla yeoi* Perkins
  - *Trinotoperla irrorata* Tillyard
  - *Illiesoperla* spp.
  - *Riekoperla tuberculata* group
  - *Riekoperla rugosa* group
  - *Riekoperla alpina* group
- Notonemouridae
  - *Austrocercella/Austrocercoides* spp.

Coleoptera
- Elmidae
  - *Simsonia* sp. L3E
  - *Notriolus quadriplagiatus* Cart.
  - *Austrolimnius* sp. L13E
  - *Austrolimnius* Group A spp.
- Ptilodactylidae
  - *Byrrocryptus* sp.
- Scirtidae
- Psephenidae
  - *Sclerocyphon maculatus* Blackburn

Megaloptera
- Corydalidae
  - *Archichauliodes* sp.

Neuroptera
- Neurorthidae
  - *Austroneurorthus* sp.

Diptera
- Tipulidae
  - Tipulidae sp. MV4
  - Tipulidae sp. MV3
  - Tipulidae sp. MV1
  - Tipulidae sp. MV10
- Chironomidae
  - *Nilotanypus* sp. MV108E
  - *Polypedilum oresitrophum* Skuse
  - *Stempellina* sp. MV58E
  - *Aphroteniella tenuicornis* Brundin
  - *Podochlus* sp. MV112E
  - *Parakiefferiella* spp.
  - *Tanytarsus* spp.
  - *Pentaneura* sp. MV7E
  - *Procladius* spp.
  - *Zavreliella* sp. MV54E
  - *Polypedilum tonnoiri* Freeman
  - *Cladopelma* sp. LTCS12
  - *Harnischia* sp. MV68E
  - *Parachironomus* sp. LTCS2
  - *Corynoneura* sp. MV63E
  - *Cricotopus* spp.
  - *Ablabesmyia* spp.
  - Orthocladiinae sp. 'grape th'
  - *Stictocladius uniserialis* Freeman
  - *Riethia stictoptera* Kieffer
  - *Rheotanytarsus* spp.
  - *Thienemaniella trivittata* Goetghebuer
  - *Podonomopsis* sp. MV71E
  - Orthocladiinae sp. MV117E
- Ceratopogonidae
  - *Bezzia* sp. RWC5
  - *Bezzia* sp. MV2
- Empididae
  - Empididae sp. MV2
  - Empididae sp. MV3
- Simuliidae
  - *Austrosimulium victoriae* Roubaud
  - *Austrosimulium furiosum* (Skuse)
- Blephariceridae

Appendix 2 ***(Continued)***

Edwardsina polymorpha Zwick
Trichoptera
Philopotamidae
Hydrobiosella spp.
Ecnomidae
Ecnomina Group E spp.
Leptoceridae
Notalina bifaria Neboiss
Hydropsychidae
Asmicridea sp. 1
Smicrophylax spp.
Austropsyche victoriana Banks
Philorheithridae
Aphilorheithrus sp.
Austrheithrus sp.
Hydrobiosidae
Apsilochorema spp.
Taschorema complex
Glossosomatidae
Agapetus spp.
Calocidae
Tamasia acuta Neboiss
Conoesucidae
Conoesucus sp. MV1
Conoesucus sp. MV10
Helicophidae
Alloecella grisea Banks

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