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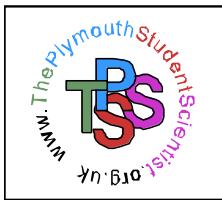
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Environmental Variables and Macroinvertebrate Community Structure in Drainage Ditches on the Somerset Levels

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Abstract

1. Studies of macroinvertebrate assemblages have tended to find relationships between environmental variables and the species present in the assemblage. Here, I looked at the relationship between assemblages and environmental variables in six drainage ditches in a small area of the Somerset Levels, UK.
2. I sampled aquatic macroinvertebrates and a range of environmental physicochemical variables from the six ditches, and investigated the differing relationships between the environmental variables and a range of assemblage datasets (overall assemblage, Coleoptera, Hemiptera, Odonata, and Mollusca).
3. Environmental variables surveyed were relatively homogeneous, with the exception of calcium, conductivity and nitrate. Diversity, species richness, and evenness for overall and single-taxon assemblages varied between sites, with no discernable pattern between large and small ditches.
4. Different taxonomic groups reacted strongly to different environmental variables, and no clear deterministic pattern is expressed, either overall or within taxa.
5. Species distributions appear to be largely due to chance, rather than significant interaction with the physicochemical environment, between ditches which are close enough together to be within the dispersal range of many taxa, and between which the chemical environment does not radically alter.

Keywords: Macroinvertebrate, ditch community, species-environment interactions.

Introduction

Ecology may be defined as the constant search for the relationships both between organisms, and between organisms and their environment. Most studies of the relationship between environmental factors and assemblages have focussed on widely-separated sites with associated gross differences in physicochemical variables, due to the differing underlying geology. For instance, Bilton et al (2006) studied sites in Hampshire (the New Forest) and Cornwall (the Lizard peninsula). At the other end of the spectrum, various studies have quantified the tolerances of individual species to single environmental variables (Bahrndorff et al. 2006), but, despite several studies which quantified the distribution of organisms, particularly macroinvertebrates, with differing environmental factors over a relatively large area (e.g. Malmqvist and Hoffsten 2000), few studies have looked at the effects of environmental variables as distribution-determining factors for organisms in the same habitat over a limited area, where assemblages would otherwise be expected to be very similar.

In addition, most studies that have studied local-scale systems have taken place in 'separated-habitat' systems of low to medium connectivity, such as ponds, lakes, and rivers (Fochetti and Argano 2006). Streams and rivers, while less obviously island-like than ponds and lakes, have only intermediate connectivity because of their unidirectional flow, which restricts the dispersal of many taxa, especially of passively-dispersing species such as gastropods (Bilton, Freeland, and Okamura 2001; Hoffman et al. 2006).

Ditches appear to be a model system for the study of local-scale environmental variations and their effects on macroinvertebrate assemblages. They are strongly human-impacted systems, constructed to move water around wet, low-lying areas such as the Somerset Levels and the East Anglian fens. Due largely to their very shallow gradients, ditches have high levels of connectivity. This means that flow rates are very low, allowing bidirectional aquatic dispersal for all species, rather than just actively-dispersing organisms such as Odonata (Patterson and Atmar 1986; Bilton et al. 2001). Furthermore, as ditches are generally managed for drainage purposes and as 'wet fences', individual ditches are interlinked with each other in a complex network, potentially allowing species to disperse rapidly to every part of the network from as little as a single introduction point (Armitage et al. 2003; Bousset et al. 2004). Consequently, the only major barrier to the homogenisation of aquatic fauna between ditches is likely to be the physicochemical

variation found within them (Foster et al. 1990; Janse and Van Puijenbroek 1998).

Ditch faunal assemblages tend to be different to those of either ponds or streams. In general, ditch assemblages tend to be less speciose than either streams or ponds, and include a mixture of lentic and lotic taxa as well as rare species not reported from other aquatic habitat types (Williams et al. 2004). This is thought to result from the unique abiotic environment of ditches, which both provides an environment suitable for different species to ponds or streams, and allows pond and stream invertebrates to use ditches as refugia (Armitage et al. 2003; Williams et al. 2004).

Studies have found significant effects of physicochemical environmental variables on macroinvertebrate assemblages when study areas are well separated: for example, the 1996 National Pond Survey (Biggs et al. 2000) found the UK-wide distribution of pond invertebrates could be described on a series of environmental axes: pH, depth/permanence, substrate/hydrology, and location.

There has been little work done on ditches, however, and little agreement between studies. Painter (1999) found that bank profile, ditch age, water depth, phosphate, nitrate, calcium, sediment depth, and plant cover had significant effects on the assemblages of ditches at Wicken Fen, Cambridgeshire; Armitage et al (2003) found that pH and the percentage cover of submerged, floating and emergent plants were important variables along a single ditch; and Foster et al (1990) found that water depth, pH, percentage cover of submerged, floating and emergent vegetation, conductivity, nitrate, and sodium levels were all significant. Using a limited set of invertebrates, a similar but non-nested set of variables is found to be important: Watson & Ormerod (2004), studying three gastropod species (*Segmentina nitida*, *Anisus vorticulus* and *Valvata macrostoma*) found that conductivity, percentage cover of emergent vegetation, calcium, alkalinity, total organic nitrogen, and chlorine were important, while Rouquette & Thompson (2005), studying the damselfly *Coenagrion mercuriale* found that percentage cover of submerged, floating and emergent vegetation, percentage of open water present, dominant substratum type, bank width, and berm width were all important.

Overall, these findings are similar to, but not nested with, the variables found to be significant for ponds at the national scale (Biggs et al. 2000). This supports the idea that waterbody type, along with broad-scale

physicochemical variations derived to a certain extent from the underlying geology, such as pH, are important in the formation of assemblages, together with location-linked factors such as the geographic range of species, and then further smaller-scale variation, such as depth, are important at the local-scale, individual ditch level.

It seems likely that environmental factors which vary significantly only over a wide geographical range will have a less significant effect on sites which are close together, and so the significant environmental factors will vary, to a certain extent, dependent on the scale at which ecosystems are studied, but this is likely to be less important than factors such as the waterbody type studied. For example, the substrate present is a factor which has been found to be significant at a nationwide scale in ponds in the UK (Biggs et al. 2000). It is, in turn, connected to the underlying geology of an area (e.g. granite boulder-strewn uplands or fertile silt plains), as well as on the aspect of the land, which is in turn dependent to some extent on the underlying rock forms: when substrate type has been artificially changed at a local scale in rivers, assemblages present on each substrate type were found to be significantly different (Brunke, Hoffmann, and Pusch 2002).

Of more importance at a limited scale, within the dispersal range of many organisms, are likely to be factors which do vary significantly within a local area. For example, depth will fluctuate at whatever scale is sampled, even across a single waterbody: it has been found to alter the species composition of *Lestes* damselfly larvae along a depth / permanence gradient (Stoks and Mcpeak 2003a; Stoks and Mcpeak 2003b). Indeed, depth seems to be the single most significant factor across many studies (e.g. Foster et al. 1990; Janse and Van Puijenbroek 1998; Malmqvist and Hoffsten 2000; Cooper et al. 2005; van der Valk 2006), and is likely to have a significant effect on other important variables: for example, temperature and oxygen content (which are themselves linked).

It is likely that different variables will differentially affect organisms. For example, molluscs are more dependent on levels of available calcium than are organisms such as hemipterans which do not build calcium carbonate shells, and consequently have limited distribution in soft-water areas such as Cornwall (Turk, Meredith, and Holyoak 2001). In general, it has been found that species within families react in generally similar ways to environmental gradients (Bilton et al 2006), although adaptations of certain species can make them anomalies within the

group. An example would be the siphons of *Ranatra linearis* Linnaeus and *Nepa cinerea* L., allowing them to breathe atmospheric air without moving from, for example, refugia in the weeds. This sets them apart from other hemipterans in terms of dissolved oxygen tolerance: while other hemipterans can utilise atmospheric air, the siphons of *R. linearis* and *N. cinerea* provide a considerable advantage to these species not enjoyed by other species which must keep moving to and from the surface, an energetically costly strategy which engenders a considerably greater risk of predation (Maitland 1978; Marklund, Blindow, and Hargeby 2001).

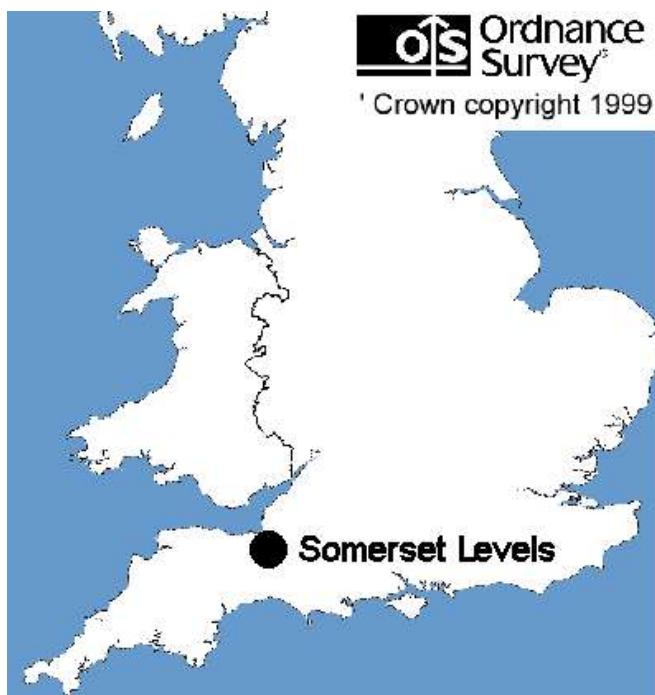
The hypothesis tested here is that, at a local scale, environmental factors will have a significant effect on macroinvertebrate assemblages. It is predicted that the most important of these will be depth and dissolved oxygen content (despite the constant variation of DO levels), due to the pervasive influence depth has on other variables, and the importance of dissolved oxygen levels to aerobic aquatic organisms such as invertebrates, especially those such as Ephemoptera and Odonata which are dependent upon oxygen dissolved in the water column rather than being able to make use of atmospheric oxygen at the water's surface. Although DO levels do vary on a daily, even hourly basis, they must remain within the tolerances of species present at the site.

Therefore, it is also predicted that different organism groups will respond most strongly to different environmental variables, due to physiological constraints (Rundle et al. 2002). For example, pulmonate Gastropoda and Ephemoptera would be predicted to respond differently to a high concentration of nitrates and phosphates: this usually characterises eutrophic ditches with abundant macrophyte growth and low dissolved oxygen levels. The air-breathing, macrophyte-feeding snails would be expected to prosper in the environment, while the Ephemoptera, filtering oxygen from the water column via abdominal gills, would not be able to withstand the reduced dissolved oxygen levels, and so would be present in severely reduced quantities compared to the massively increased snail populations.

Methods

Study sites

This study was conducted on the Somerset Levels (see Fig. 1). This area is an internationally important



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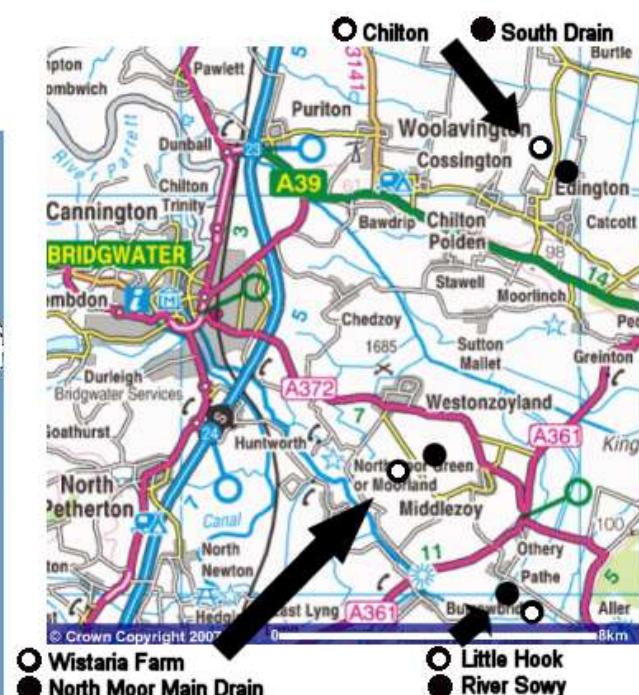


Fig. 1. Locations of the six study sites in the Somerset Levels, UK

wetland, with low-lying clay geology. It is primarily used for agriculture, especially cattle grazing, and for drainage purposes the entire area is criss-crossed with a network of ditches. These vary in size from small ditches draining a single field, to large ditches tens of meters wide. Larger ditches tended towards the characteristics of lowland rivers: wide, slow-flowing and with high levels of autochthonous inputs (Vannote et al. 1980), and have greater flow rates than the smaller ditches, which had no appreciable flow. I sampled at three large and three small sites (see Table 1). Across all size classes many of the vegetation types were constant, notably emergent beds of *Typha latifolia* L. (greater reedmace), *Juncus* and *Carex* species, and submerged stands of various similar pondweeds. However, some sites had unique vegetation characteristics: for example, *Lemna* spp. domination.

Sampling method and taxon identification

Ditch sampling took place in September 2006, when most aquatic and semi-aquatic macroinvertebrates are present in the environment. It has been found in other studies that data from a single season are sufficient to compare the relative assemblage composition of sites

(Bilton et al. 2006). Ditches were sampled using a hand net (1 mm mesh, dimensions 20 X 25 cm). At

each site, three metre-long non-overlapping samples were taken from a five-metre stretch of ditch. Each sample consisted of three standardised sweeps, each comprising approximately 10s of back-and-forth netting over the same area of habitat, stratified between different habitat and vegetation types available, including marginal vegetation, where present. This sampling method has been proven to allow robust comparison between assemblages at different sites, as it consistently samples between 60 and 80% of the available macroinvertebrate species pool, so giving a reliable comparative measure of species richness and biodiversity per site (Foggo, Rundle, and Bilton 2003; Bilton et al. 2006). Sweeps were pooled and preserved in 90% ethanol, leaving 18 samples across 6 sites.

50% sub-samples (by mass) were sorted and Coleoptera (excluding larvae), Odonata, Hemiptera, Ephemoptera, macrocrustacea, Hirudinea, Arachnida, Sialidae, and Mollusca (excluding *Pisidium* spp.) were identified to species level. Dipteran and coleopteran larvae, together with *Pisidium* mussels, were identified to genus level, while Chironomidae were only identified to family level.

	Wistaria Farm	North Moor Main Drain	Little Hook	Sowy River	Chilton Drain	South Drain
Width (m)	2	6	1.8	16.1	1.9	22
Depth (cm)	65	70	45	130	50	110
pH	7.78	7.65	7.10	7.77	7.48	8.04
% O ₂ saturation	40.2	37.1	22.9	45.0	8.5	44.2
O ₂ (mg L ⁻¹)	4.08	3.59	2.26	4.28	0.84	4.13
Conductivity (µS cm ⁻¹)	0.757	0.665	0.811	0.829	0.775	0.765
Temperature (°C)	14.50	16.80	15.69	17.68	15.38	18.48
Particulates (ppt)	0.37	0.33	0.40	0.41	0.38	0.38
Ca mg L ⁻¹	50.61	45.45	63.73	102.62	91.14	89.50
Mg mg L ⁻¹	3.21	7.20	3.72	5.51	5.78	8.78
Nitrate mg L ⁻¹	8.193	1.516	1038.600	7.788	4.240	0.479
Phosphate mg L ⁻¹	<0.001	0.501	0.864	0.764	0.449	0.239
Diversity (Simpson's 1-λ)	0.83	0.87	0.68	0.77	0.92	0.85
Evenness (Pielou's J')	0.67	0.72	0.55	0.57	0.83	0.70
S (Mollusc)	11	13	9	12	5	14
S (Coleoptera)	9	15	11	14	9	10
S (Hemiptera)	6	2	2	4	7	3
S (Odonata)	8	4	2	6	9	8
S (Total)	44	46	39	44	48	44

Table 1. Mean environmental and assemblage values for the six study sites on the Somerset Levels. S = species richness.

Before sampling, environmental variables were recorded from each site. A Solomat 520 C probe (Zellweger Analytics, Poole, UK) was used to record pH, temperature-adjusted conductivity, temperature, particulates, and O₂ content (mg/l and % saturation) on site. Two water samples were taken from each site in acid-washed polypropylene bottles for analysis of nutrient and metal ion content. Calcium and magnesium cation contents were analysed using atomic absorption spectroscopy (Varian SpectrAA 50B Atomic Absorption Spectrometer : Varian Ltd, USA); these metals were chosen for their biological importance to organisms (Watson and Ormerod 2004; Bilton *et al.* 2006). Nitrate and phosphate levels were measured using a Dionex autoanalyser (Camberley, UK). Width and depth were estimated (mean of five measurements) after sampling at each site (Table 1).

Data analysis

Five datasets were created: a standard dataset consisting of abundance data for all identified taxa, for all samples at all sites, and four alternative datasets: abundance data at all sample sites for Mollusca, Coleoptera, Hemiptera, and Odonata.

I first quantified the biodiversity and evenness of each sample using Simpson's index of biodiversity, and Pielou's evenness index in Primer 5.2.9 for Windows (Clarke and Gorley 2001). A similarity matrix was constructed for each dataset, using the Bray-Curtis coefficient on untransformed counts for all taxa present in each dataset, and the significance of between-ditch differences was then tested in Primer using ANOSIM. A further ANOSIM was then performed to test for the significance of differences in assemblages between the large (>5m wide) and small (<5m wide) ditch categories.

Table 2. Analysis of similarity results: assemblage similarity between sites, and between ditches classified as large (width >5m) or small (width <5m).

Dataset	Test statistic, Global R (p-value)	
	Site	Size
Overall assemblage	0.881 (0.001)	0.228 (0.005)
Coleoptera	0.642 (0.001)	0.642 (0.001)
Hemiptera	0.564 (0.001)	0.539 (0.001)
Mollusca	0.878 (0.001)	0.878 (0.001)
Odonata	0.779 (0.001)	0.655 (0.001)

Multidimensional scaling (MDS) was performed to generate two-dimensional visual representations of the differences between samples, ditches, and ditch classifications (big or small), in terms of the assemblages in all five datasets. A second-stage MDS analysis was carried out to assess the concordance of the taxonomic datasets with the overall assemblage: this technique generates a second stage similarity matrix based on the correlation between similarity matrices from alternative datasets, producing a similarity matrix of similarity matrices. An MDS ordination was then produced from this second-stage matrix, providing a two-dimensional representation of the relative contributions of the alternative datasets, and hence the different orders, to the overall, combined dataset.

Primer was then used to perform a Simper analysis, to quantify the within-site-class similarities and between-site-class dissimilarities, and assess which species were driving the differences between large and small ditches.

To determine whether different taxa respond to environmental variables in different ways, assemblage-environment relationships were examined for all datasets using CANOCO for Windows (Ter Braak and Smilauer 1998). Canonical correspondence analyses (CCAs) were carried out on all datasets, and significance of species-environment interactions was quantified via a Monte Carlo test with 499 permutations. This allowed the responses of Molluscs, Coleoptera, Hemiptera, and Odonata to be assessed.

Results

Ditches sampled were relatively homogeneous in terms of environmental variables, with the exception of conductivity, which ranged from 0.665 to 765 µS (adjusted for temperature), calcium (45.45-102.62 mg/L), and nitrate (0.479-1038.6 mg/L) (Table 1). Also, ditch width and depth varied between the large and small ditches as expected.

Diversity and evenness vary widely between sites (Table 1). Diversity (Simpson's diversity index, $1-\lambda$) ranged from 0.68 (Little Hook) to 0.92 Chilton drain),

while Pielou's evenness index, J' , ranged from 0.55 (Little Hook) to 0.83 (Chilton).

A total of 98 species were recorded from the six ditches, with each ditch containing between 35 and 48 species. In terms of species richness, Coleoptera dominate the assemblage, with 35 species present. Molluscs were also relatively speciose, with 18 species present, while Odonata and Hemiptera were relatively species-poor, with 11 and 7 species respectively. Crustacea, while only having two species present, had both in very high abundance, especially at the smaller sites.

Analysis of similarity (ANOSIM) found a significant difference between ditches individually, and between ditches classified as big or small, for all datasets ($p = 0.001 - 0.005$) (Table 2). Visual inspection of the data, via multidimensional scaling (MDS) plots, reveals that there is clustering by site (Fig. 2), and less distinct clustering of ditches classified as big or small (Fig. 3), which in general consisted of larger sites exhibiting relatively little variation and smaller sites varying more widely.

At the level of the individual taxonomic groups, molluscan assemblages per sample are clustered into non-overlapping groups by site (Fig. 2), with the three large sites (Fig. 3) (North Moor Main Drain, South Drain, and Sowy River) relatively tightly clustered with a small site, Wistaria Farm, while the other two small sites, Chilton Drain and Little Hook, are distinctly different to the group, with Chilton much further away than Little Hook. In Hemiptera, a similar but less distinct pattern is found, although the Sowy samples overlap those from South Drain (Fig. 2), and, although the Wistaria Farm samples cluster with the three large ditch samples, there is no overlap between large and small ditch classes (Fig. 3). As with Mollusca, Little Hook and Chilton are the most separate from the cluster.

With Odonata, a slightly different pattern is observed. At a site-specific level (Fig. 2), North Moor Main Drain and Little Hook form distinct, non-overlapping clusters, but Sowy River samples overlap those from South Drain, and Chilton

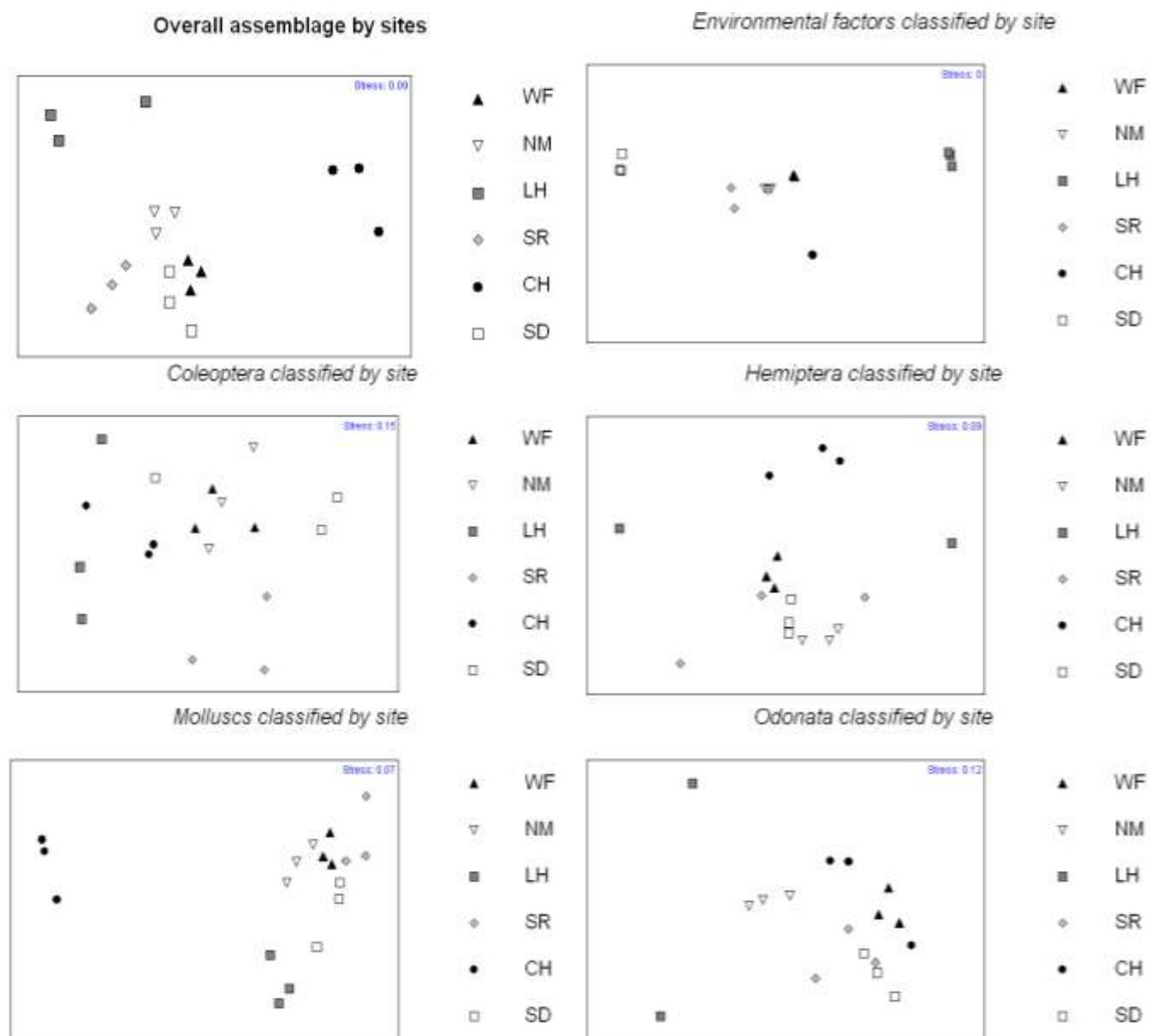
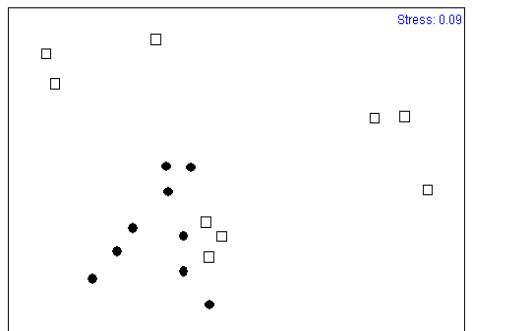


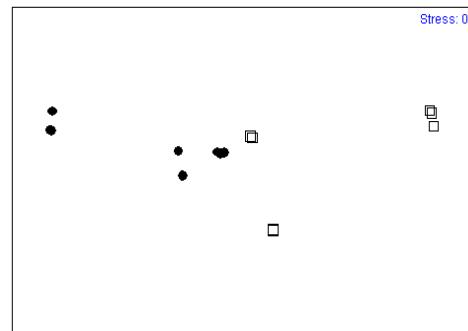
Fig. 2. Multidimensional scaling (MDS) ordinations of all environmental and assemblage datasets, classified between sites. WF = Wistaria Farm, NM = North Moor Main Drain, LH = Little Hook, SR = Sowy River, CH = Chilton, and SD = South Drain. Hemiptera and Odonata both only have two symbols at Little Hook, due to the occurrence of identical assemblages.

Overall assemblage by size classification



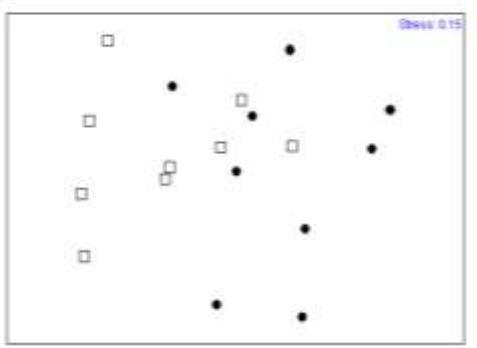
Coleoptera classified by ditch size

Environmental factors classified by size

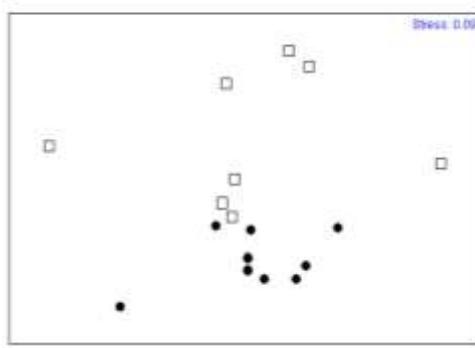


Small
Large

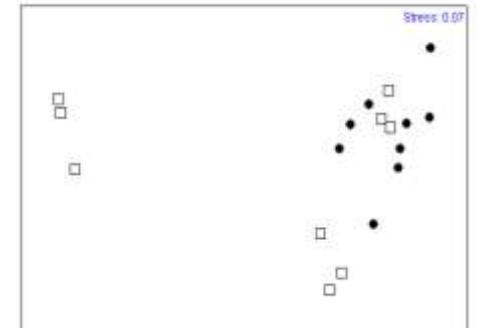
Hemiptera classified by ditch size



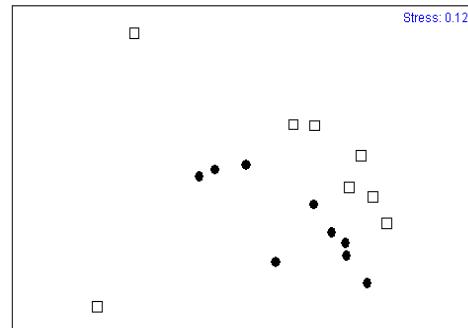
Molluscs classified by size



Odonata classified by ditch size



Small
Large



Small
Large

Fig. 3. Multidimensional scaling (MDS) ordinations of all environmental and assemblage datasets, classified between large (width >5m) and small (width <5m) ditches. WF = Wistaria Farm, NM = North Moor Main Drain, LH = Little Hook, SR = Sowy River, CH = Chilton, and SD = South Drain.

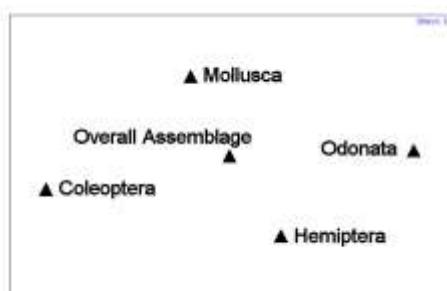


Fig. 4. Two-stage MDS ordination showing the relationships between taxonomic datasets and the overall assemblage dataset

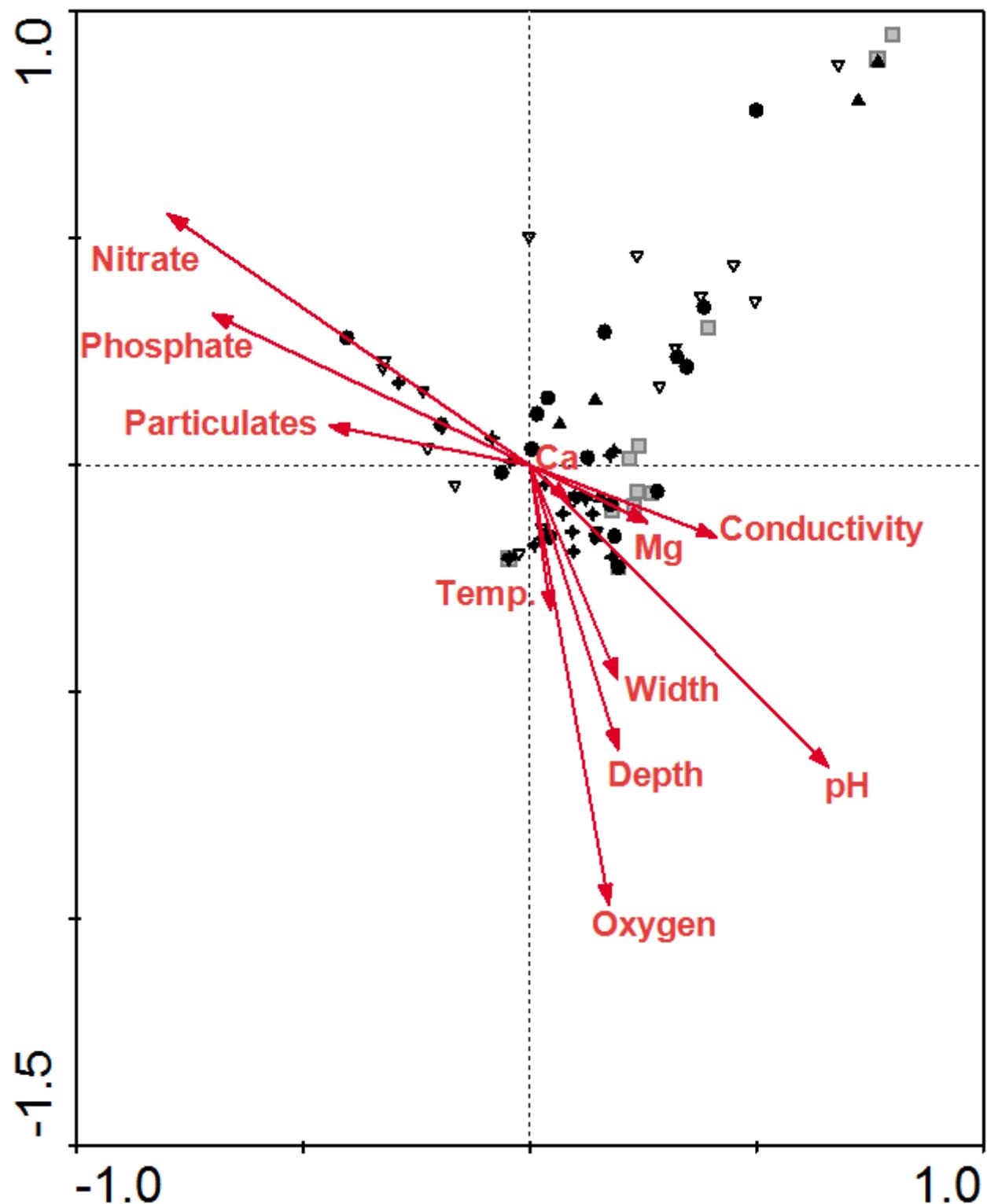


Fig. 5. Canonical Correspondence Analysis ordination for all taxa, all sites species-environment relations. Graph symbols are Hemiptera: up-triangle (filled); Mollusca: filled star; Odonata: filled square; Coleoptera: down-triangle (empty); Miscellaneous: filled circle.

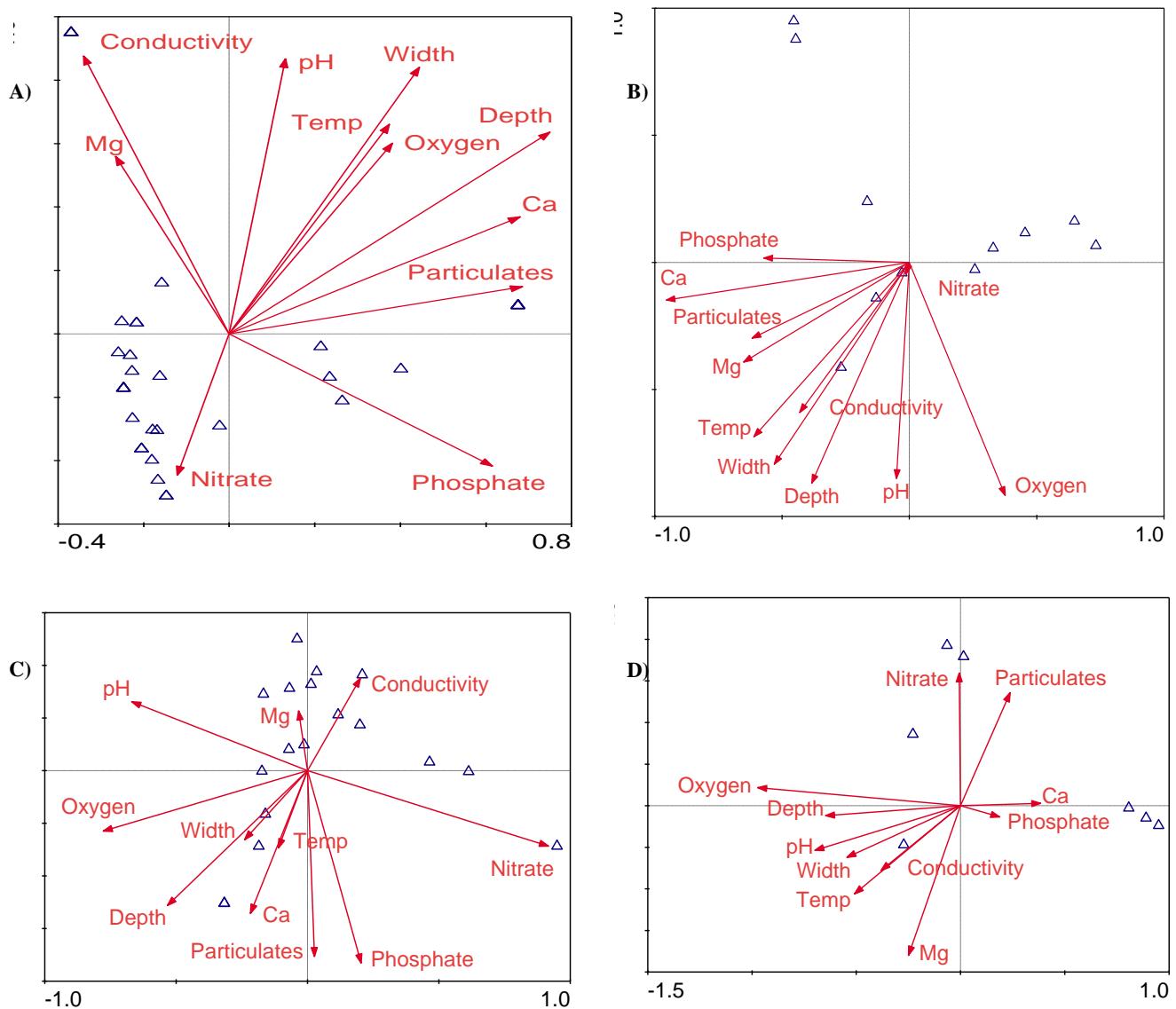


Fig. 6. Canonical Correspondence Analysis ordinations for different taxonomic databases, all sites. A) = Coleoptera, B) = Odonata, C) = Mollusca, D) = Hemiptera.

samples overlap samples from Wistaria Farm. Odonata exhibit strong separation by size class, albeit with one sample from Little Hook causing the two groups to overlap (Fig. 3). The small-ditch samples show considerably greater variation than do the large ditches, which are relatively tightly clustered.

Coleoptera exhibit the least clustering by site (Fig. 2), and only Chilton and Sowy River do not overlap the samples of at least one other site, although Chilton is itself overlapped by Little Hook. There is a gradation from small sites to large sites (Fig. 3), which is relatively clear, despite the samples from Wistaria Farm overlapping those of both South Drain and North Moor Main Drain.

Second-stage MDS analysis of the relative contributions of different faunal groups (Mollusca, Coleoptera, Hemiptera, and Odonata) revealed that all four had completely different influences on the overall assemblage makeup (Fig. 4), and were approximately equidistant from each other and from the overall assemblage.

To quantify the within-group similarities and between-group dissimilarities, and identify the major species-level drivers, Primer was used to carry out SIMPER analyses of assemblage data classified by ditch size (Table 3). The crustaceans *Asellus aquaticus* L. and *Crangonyx pseudogracilis* Bousfield, together with the snails *Bithynia tentaculata* L. and *Anisus vortex* L. were

Table 3. SIMPER analysis of within-group similarity and between-group dissimilarity, for ditches classified as large (width >5m) or small (width <5m)

Small				Large			
Species	Mean abundance	Contribution n	Cumulative contribution	Species	Mean abundance	Contribution	Cumulative contribution
<i>A. aquaticus</i>	172.67	21.54%	21.54%	<i>B. tentaculata</i>	88.89	22.38%	22.38%
<i>C. pseudogracilis</i>	55	13.61%	35.14%	<i>C. pseudogracilis</i>	98.44	21.92%	44.29%
<i>B. tentaculata</i>	62.56	11.29%	46.43%	<i>A. vortex</i>	133.11	17.67%	61.96%
<i>R. peregra</i>	14.67	9.15%	55.58%	<i>A. aquaticus</i>	96.44	14.31%	76.27%

Large and small		Mean dissimilarity = 64.66%			
Species	Mean abundance (small)	Mean abundance (large)	Contribution	Cumulative contribution	
<i>A. aquaticus</i>	172.67	96.44	21.08%	21.08%	
<i>A. vortex</i>	34.67	133.11	15.26%	36.34%	
<i>C. pseudogracilis</i>	55	98.44	13.49%	49.84%	
<i>B. tentaculata</i>	62.56	88.89	13.41%	63.24%	

Table 4. Strength of CCA correlations between assemblages and environmental variables. Figures in bold are correlations stronger than +/- 0.5.

Assemblage	1st environmental axis	pH	Nitrate	Phosphate	Depth	Width	Particulates	Ca	Mg	Temperature	Oxygen content
Overall	0.9837	0.6474	-0.7844	-0.6886	0.1907	0.1896	-0.4143	0.0855	0.4043	0.0454	0.1708
Coleoptera	0.9893	0.1300	-0.1199	0.6085	0.7420	0.4395	0.6782	0.6728	-0.2629	0.3706	0.3772
Odonata	0.9600	-0.0487	-0.0119	-0.5497	-0.3690	-0.5092	-0.5934	-0.9171	-0.6254	-0.5866	0.3612
Mollusca	0.9632	-0.6447	0.8839	0.1917	-0.5138	-0.2310	0.0259	-0.2092	-0.0324	-0.1062	-0.7491
Hemiptera	0.9963	-0.6967	-0.0067	0.1876	-0.6458	-0.5438	0.2369	0.3831	-0.2489	-0.5067	-0.9693

the main drivers of both similarity and dissimilarity when ditches are classified as large or small (Table 3). CANOCO was then used to perform CCAs for all datasets, to investigate species-environment relations for the overall assemblage dataset (Fig. 5), and for each of the four taxonomic datasets (Fig. 6). Strength of the species-environment relationship was determined to be significant using a Monte Carlo test with 499 permutations (total CCA: $p = 0.002$ for all datasets). CCA found that the overall assemblage (Fig. 5) responded differently to the taxonomic groups (Fig. 6), which in turn responded most strongly to different environmental variables (Table 4). The first species axis for the overall assemblage (Fig. 5) is strongly correlated with the first environmental axis and pH, and strongly

negatively correlated with nitrate and phosphate. The first coleopteran species axis (Fig. 6a) was strongly correlated with environmental axis 1, depth, particulates, calcium, and phosphate, with no strong negative correlations. The first Odonata species axis (Fig. 6b) is strongly correlated with environmental axis 1, and strongly negatively associated with calcium, magnesium, particulates, temperature, phosphate, and width. Molluscs (Fig. 6c) were strongly correlated with environmental axis 1 and nitrate, and strongly negatively associated with oxygen content, pH, and depth. Finally, the first Hemiptera axis (Fig. 6d) was strongly correlated with environmental axis 1, and negatively associated with oxygen content, pH, depth, width, and temperature.

Discussion

Overall, it was found that ditches differed significantly from each other in terms of both the overall abiotic environment and the assemblages present at each, a finding consistent with that of Painter (1999). No intrinsic difference between large and small ditches was found for assemblages, despite clear separation in terms of the overall abiotic environment, although two eutrophic ditches (Little Hook and Chilton) were clearly separate both from each other and from the other four sites.

Diversity and evenness vary widely across sites, but large ditches varied less than smaller sites: however this also seemed to be influenced more by the eutrophic state of two of the three smaller ditches than by size, as the small non-eutrophic ditch (Wistaria Farm) had very similar scores to the large (non-eutrophic) ditches. The two eutrophic sites, Chilton and Little Hook, had the highest and lowest diversity and evenness scores, respectively. Little Hook was a eutrophic site with virtually no submerged or emergent vegetation due to the complete *Lemna* coverage, while Chilton, the most diverse site, was less eutrophic, and dominated by emergent macrophytes. This fits the pattern of submerged and emergent vegetation correlating positively with diversity, and surface vegetation correlating negatively (Foster *et al.* 1990; Cattaneo *et al.* 1998; Malmqvist and Hoffsten 2000; Mcabendroth *et al.* 2005b).

There appears to be no intrinsic barrier to species dispersal between large and small ditches; rather, the indirect effects of environmental factors affect the species present in assemblages. For example, high nitrate levels at Little Hook have led to eutrophication and high levels of surface vegetation (*Lemna* spp.). This has led to decreased dissolved oxygen levels at the site, which have in turn caused the low occurrence of Hemiptera and Odonata in the ditch. Both of these groups are largely dependent on dissolved oxygen, rather than atmospheric air, to breathe, and so cannot survive at the site. In fact, the two species of Hemiptera found at the site, *Nepa cinerea* and *Ranatra linearis*, both breathe atmospheric air via a siphon,

instead of absorbing oxygen through the water.

Large ditches are a more stable environment: while it is possible for small ditches to have similar assemblages to the larger ditches when in good condition, they are more vulnerable to disturbances, such as eutrophication or pollution (Janse and Van Puijenbroek 1998). This lack of buffering capacity has the effect of making small ditches a more unstable environment, and so, although large-ditch type assemblages can exist in small ditches, they are at a more unstable equilibrium (Evensizer and Turner 2006).

The taxonomical group that follows most closely the pattern exhibited by the environmental factors was Mollusca (Fig. 3, 6). This was expected: unlike the other taxonomic groups studied, molluscs have no actively-dispersing life stage, and so are likely to be more correlated with the environmental factors than are those species such as Coleopteran adults which can use more unfavourable environments as a 'rest stop', rather than being constrained to the same degree as the passively-dispersing molluscs (Bilton *et al.* 2001). However, molluscs have problems when considered as a large-scale habitat-monitoring tool: they are limited in their countrywide dispersal by large-scale habitat requirements for pH and calcium. For example, the molluscan fauna of Cornwall, a soft water area, is relatively depauperate (Turk *et al.* 2001) when considered against a neutral to basic area such as my study site, the Somerset Levels.

Assemblages show considerable overlap when compared between sites (Fig. 2), and less so when compared between large and small ditches (Fig. 3). However, when large and small ditches are in equivalent condition, e.g. non-eutrophic, assemblages appear not to be significantly different between size classes: Wistaria farm, a small site, exhibited a similar assemblage to those of the large sites at South Drain, River Sowy, and North Moor Main Drain. The assemblage present at Little Hook contained virtually no Odonata or Hemiptera, probably due to the decreased dissolved oxygen content, as a result of the eutrophication and consequent *Lemna* domination of that site. A two-stage MDS plot

of taxonomic groups (Fig. 4) revealed that all four taxonomic groups explicitly tested had nearly diametrically opposed ordinations about a central point, the overall assemblage value. Odonata and Hemiptera were slightly closer to each other than they were to Mollusca and Coleoptera, but the groups were virtually equidistant from each other and from the overall assemblage point.

Largely due to the Little Hook result, Odonata and Hemiptera exhibited stronger dissimilarities between large and small ditches (Fig. 3) than did Mollusca or Coleoptera, which differed largely in abundance between the size classes.

SIMPER analysis of within-group similarity and between-group dissimilarity, for size groups (Table 3), showed that four species – *Asellus aquaticus*, *Crangonyx pseudogracilis*, *Anisus vortex*, and *Bithynia tentaculata* – were the main drivers of similarities and dissimilarities between large and small ditches. These organisms, two molluscs and two crustaceans, are likely to be more strongly constrained by environmental factors, due to their inability to disperse actively from the environment (Bilton *et al.* 2001), indicating a possible physicochemical factor influencing populations.

In order to quantify the species-environment relationship, CANOCO was used to carry out CCAs on overall assemblage data (Fig. 5), and on single-group taxonomic assemblage datasets (Fig. 6). Of the species that were of primary importance in the SIMPER analysis, the two crustaceans, *A. aquaticus* and *C. pseudogracilis* were not strongly associated with any environmental variables, although they did exhibit a minor positive relationship with phosphate and nitrate levels, which covaried with each other. *B. tentaculata* also did not exhibit strong environmental relationships, while *A. vortex* showed a preference for wider and deeper ditches, but not for any measured chemical variables.

Overall, species in the CCA tended to not exhibit strong environmental preferences (Fig. 5), instead clustering in the centre of the ordination, close to the origin. Although this seems at odds with previous studies, particularly those on ponds (e.g. Biggs *et al.* 2000; Bilton *et al.* 2006), this is likely to result

from the relative homogeneity of environmental variables in the Somerset Levels ditches studied here, due to their proximity and near-identical underlying geology and riparian land use environment. It is also indicative of the different structuring factors present in ditches when compared to ponds. It is worth noting that molluscs, the most environmentally-dependent taxon studied, shows the greatest correlation with the few environmental factors which were found to vary significantly between sites; particularly calcium and nitrate.

Also potentially influencing the species-environment relationships found are species which were only found at one site, for example *Halipplus immaeulatus*, *Laccophilinae hyalinus*, *Peltodytes caesus*, *Potamopogyrus antipodarum*, and *Viviparus contectus*. These will exhibit potentially excessive correlation with the factors present at the site they were from – while this could be symptomatic of a limiting environmental factor, it is more likely to be due to chance effects of dispersal, whereby environmental conditions are not constraining the species to a single site, but rather a species tolerant of a wide range of conditions has not yet dispersed as widely as it is physiologically capable of (Bilton *et al.* 2001). Even in highly-connected, networked sites, such as the Somerset Levels, species, especially passively-dispersing, near-sedentary species such as molluscs, will take time to maximise their realised ecological niche. This is confounded further when species on the edge of their range, such as *V. contectus*, or are present only as a single individual at a site, such as *Theodoxus fluviatilis*, are present, as this will give a false impression of the ideal conditions for the species, when in fact it may just be hanging on in relatively unfavourable conditions.

The lack of any significant correlation of overall and single-taxon assemblages, or even most species, with environmental factors, strongly suggests that, at the small scale studied, individual assemblage makeup is due to chance, rather than any deterministic, limiting, factors. While broader-scale variation in abiotic factors such as pH (e.g. Biggs *et al.* 2000), and between-waterbody type variations such as flow rate (as in Malmqvist and Hoffsten 2000), as well as the differences implicit in different waterbody types, e.g. the

differential connectedness of ponds, streams and ditches (Ribera, Foster, and Vogler 2003;Mcabendroth *et al.* 2005a), will have a part to play in the formation and composition of the regional species pool, chance dispersal events seem to be the major factor influencing the composition of assemblages at individual sites within a limited area, even in sites as well-connected to each other as the ditch network of the Somerset Levels. Larger ditches, as more permanent and stable landscape features, usually contain greater diversity, evenness and species richness, although these effects are negated somewhat in drainage ditches due to the management regime, which ensures that ditches do not usually dry out completely, even in summer when equivalent-scale, less-managed waterbodies such as ponds may well do so. For example, the Wistaria Farm study site exhibited similar assemblage parameters to those of the larger, more stable ditches. However, the physicochemical environment of smaller ditches will be considerably more variable, e.g. temperature, which may have a partially limiting effect of the species which can inhabit the sites, as I found with Hemiptera and Odonata at the highly-eutrophic Little Hook site.

Many of the species found, particularly the nationally scarce beetles, were ditch specialists (Balfour-Browne 1940;1950;1958), underlining the importance of ditches to floodplain aquatic diversity. The lack of correlation between assemblage and environmental variables should mean that this is relatively easily achievable – the ditch with lowest diversity was the duckweed-dominated, eutrophic, Little Hook, and even this site had mollusc and beetle species present comparable in number to the larger, more stable, ditches. Molluscs and crustaceans were also present in far greater abundances in this ditch than in the others, probably due to the increased food supply and decreased predator presence.

Ditches, as a highly-connected, networked environment, clearly show great potential for quantifying the environmental preferences of organisms, particularly passively-dispersing species which are more limited by accidents of dispersal in less-connected sites, such as ponds. An extension of this study to cover a greater area, and thus a greater range of both

environmental variation and species recorded would seem to be the logical next step.

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