

Intrabiome Distributional Patterns of Lotic Macroinvertebrate Assemblages

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Macroinvertebrates were collected at five sites along each of three rivers within the eastern deciduous forest biome in spring, summer, and autumn. Macroinvertebrate density at sites in mixed land use areas was intermediate between high levels at sites in farmlands and low levels in forests. Cluster analysis using mean density of the 24 dominant taxa revealed three groupings of river sites each of which was consistently associated with a land use type. Clusters were poorly associated with season of collection, site location along rivers, and with specific river drainage. Hydropsychidae and Leptophlebiidae characterized forested sites. The assemblage associated with mixed land use areas included Psephenidae, Baetidae, Tricorythidae, and Heptageniidae. Farmland river sites were characterized by Ceratopogonidae, Corixidae, Oligochaeta, and Tricladida. The mixed land use group of river sites was faunistically more similar to sites in forested than in farmland areas. Forested sites were fast-flowing and had little benthic detritus; farmland sites were slow-flowing and had high levels of detritus. The biome dependency hypothesis, which predicts that similar assemblages of macroinvertebrates are likely to occur at river sites both within and among drainages if the basins occupy the same biome, was not largely supported because characteristic vegetation had been disturbed.

Des macro-invertébrés ont été recueillis au printemps, à l'été et à l'automne à cinq sites de trois cours d'eau passant par le biome de la forêt orientale à feuilles caduques. La densité des macro-invertébrés dans les sites des zones où l'on fait un usage mixte des terres se situait à mi-chemin entre les fortes densités des sites des zones agricoles et les faibles densités des sites des zones forestières. L'analyse en grappes sur la base d'une densité moyenne de 24 taxons dominants a fait ressortir trois groupes de sites de rivières qui ont été chacun systématiquement associés à un type d'utilisation des terres. Les grappes n'ont été que faiblement associées avec la saison de collecte, l'emplacement des sites le long des cours d'eau et le débit de ceux-ci. On a surtout capturé des hydropsychidés et des leptophlebiidés dans les sites forestiers. Dans les zones faisant l'objet d'une utilisation mixte, on retrouvait surtout des psephenidés, des baetidés, des tricorythidés et des heptageniidés. Les sites des zones agricoles étaient dominés par des ceratopogonidés, des corixidés, des oligochaetidés et des tricladidés. La faune des groupes de sites choisis dans la partie d'utilisation mixte des sols ressemblait davantage à celle des sites des zones forestières qu'à celles des zones agricoles. Les sites des zones forestières se trouvaient à des endroits où le débit est rapide et les quantités de détritiques benthiques y étaient faibles; les sites des zones agricoles étaient quant à eux à des endroits où le débit est lent et l'on y trouvait des quantités importantes de détritiques. L'hypothèse de dépendance face au biome, qui précise que l'on trouvera très probablement des assemblages similaires de macro-invertébrés le long des rivières au sein de mêmes bassins versants et entre les bassins versants si ceux-ci occupent le même biome, n'a pas été véritablement confirmée parce que la végétation typique a été perturbée.

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One goal in ecology is the identification of factors that determine the abundance and distributional patterns of organisms (Andrewartha and Birch 1954, 1984). Historically, the described empirical relationships between riverine fauna and environmental factors were based on the classification of rivers partitioned into discrete units or zones from headwaters to mouth (Hawkes 1975). However, predictability of such models was poor when relationships were applied to rivers away from the original study area. The applicability of relationships to other study areas depends on environmental components and scale (Seifert 1984) as well as taxonomic resolution.

More recently, the importance of riparian vegetation and adjacent forests has been recognized in terms of energy inputs to streams (Fisher and Likens 1973; Hynes 1975). In devel-

oping the river continuum concept, Vannote et al. (1980) used drainage basin as a framework within which a continuously integrated series of physical gradients along a river were associated with changes in functional feeding groups of macroinvertebrates. They suggested that changes in feeding guilds of macroinvertebrates reflected the relative contribution of autochthonous and allochthonous inputs and transport of organic matter along rivers that originate in forested areas. Accordingly, several workers have emphasized the importance of riparian vegetation in structuring macroinvertebrate communities in streams (Cummins et al. 1984, 1989); however, the influence of the land (throughout the drainage basin) on stream biota has received less attention (but see Woodall and Wallace 1972; Molles 1982; Whittier et al. 1988). Additionally, the seasonal influence of climate and terrestrial vegetation on the life

history strategies of lotic macroinvertebrates at north temperate latitudes has been well documented (Hynes 1970; Rosenberg 1979). Changes in numbers and biomass of invertebrate taxa that follow particular life history strategies reflect latitudinal or altitudinal changes in temperature and available food sources (Clifford 1982).

Corkum (1989) evaluated the relative importance of biogeographical (landscape) and on-site hydrological variables on the spatial distribution of benthic macroinvertebrates at 100 river sites throughout northwestern North America. Although both types of variables contributed to the correct classification of site groupings characterized by distinct fauna, landscape features were more useful than hydrological variables in discriminating among site groupings. Such findings are of value in ecology because they permit one to anticipate the community composition of macroinvertebrates occurring at river sites from landscape information on maps.

Ross (1963) showed that there was a strong correspondence between distributional patterns of trichopteran larvae in small rivers and the terrestrial biome (defined by climate, but reflected by vegetation). Some caddisfly species were endemic to rivers in the western montane forests, whereas other species occurred only in rivers of the eastern deciduous forests. Although biomes appear to be an important determinant of broad-scale distributional patterns of lotic macroinvertebrates (Ross 1963; Wiggins and Mackay 1978; Corkum 1989), local and regional land use also influence the biotic structure and function of streams (Resh et al. 1988).

Expanding on earlier work by Ross (1963), Corkum (1989) suggested that similar assemblages of macroinvertebrates were most likely to occur at river sites within or among drainage basins if the basins occupied the same biome. This idea of similarity of macroinvertebrate distributional patterns within and among drainage basins differs from the more accepted view of faunal changes occurring along the length of a river (Hawkes 1975; Vannote et al. 1980).

In the present study, I examine whether or not significant, consistent differences occur among macroinvertebrate communities at river sites within a biome. A subsequent study will compare spatial patterns of macroinvertebrate communities in streams within and among biomes. I sampled macroinvertebrates and measured associated environmental factors at five sites along each of three rivers flowing through agricultural croplands and forested areas in the eastern deciduous forest biome during spring, summer, and autumn. If distributional patterns of lotic macroinvertebrate assemblages do differ among river sites within a biome, I wished to determine whether the patterns most strongly reflect (a) the season during which animals were collected; (b) the relative position of a site along the length of river; (c) the land through which rivers flow; or (d) the river within the biome. Using multivariate statistics, I identified groups of river site samples characterized by distinct macroinvertebrate assemblages, and examined each group for consistency with respect to sample season, site location, type of land use and river. I then evaluated which environmental variables best delineated the groups characterized by the assemblages.

Materials and Methods

Study Area

The Credit, Ausable, and Maitland rivers, located in southwestern Ontario, were each sampled at five locations along

their length in spring (12–20 May), summer (20–24 July) and autumn (6–9, 16–17 October) 1987 (Fig. 1). The three drainages occur within the eastern deciduous forest biome (Udvardy 1975; Danks 1979).

These rivers were chosen because they were not interrupted by reservoirs and no major industrial development occurred within the drainage basins. Towns were present in all drainages, but urban centres were restricted to areas below the most downstream sampling location. All drainages were located on Palaeozoic (sedimentary) bedrock (Chapman and Putnam 1984). In addition, drainage basins were selected within a limited latitudinal range (43°04' to 43°54'N) (Fig. 1) to reduce variation in life history development for any given taxon.

The Credit River, which drains an area of 843 km², rises in a hilly area of moraines and flows south through deciduous forests for about 95 km before entering Lake Ontario at Port Credit west of Toronto. The Credit River drops 415 m from its source to Lake Ontario at an average slope of 0.0044 m/m. The Ausable River, which drains an area of 1645 km², follows a depression in front of a glacial moraine (Chapman and Putnam 1984) and flows into Lake Huron at Grand Bend. The river drops 149 m from its source to Lake Huron at an average slope of 0.0020 m/m. The Maitland River drains an area of 2521 km² of glacial till and clay plain and enters Lake Huron at Goderich, north of Grand Bend. I sampled the main, northern branch of the Maitland River, which flows for about 144 km. Over this distance, the river drops 272 m from its source to the lake at an average slope of 0.0020 m/m. Both the Ausable and Maitland rivers flow through agricultural croplands.

Sample sites (numbered sequentially from upstream [site 1] to downstream [site 5]) were selected along river lengths (Fig. 2). Site locations corresponded whenever possible to gauging stations (Water Resources Branch, Environment Canada). By chance, most river sites were sampled at low flow in spring, summer, and autumn (Fig. 3). However, during the summer, two downstream sites (4 and 5) on the Credit River were sampled 1 d after a local storm.

River widths at sample sites ranged from 6 to 75 m, corresponding to stream orders 3–7 (cf. Cummins 1975a). Recently, Hughes and Omernik (1981) stressed the imprecision of using stream order to represent size and width of rivers. Moreover, the effect of map scale on stream order (especially on low order streams) is well known (Leopold et al. 1964). Accordingly, I elected to use stream width rather than order as it is a direct and easily obtained measure of river size.

Sampling Procedures

River sites were sampled (within a 50 m section of river length) in spring, summer, and autumn. Because of growth and emergence of various aquatic insects (insects dominated the samples) throughout the year, I assumed that the 45 collections (15 river sites × 3 seasons) were independent.

The on-site environmental variables selected for measurement (minimum and maximum water temperature, conductivity, pH, dissolved oxygen, suspended sediments, ash free dry mass of sample detritus, river width, substrate type, riparian cover, bank stability, mean depth, mean current velocity) were shown previously to be important in the distribution of macroinvertebrates (Hawkes 1975; Pennak 1977; Vannote et al. 1980).

Maximum and minimum water temperatures were obtained for each site in each season sampled. At each sample site, a maximum-minimum thermometer was set in the river and

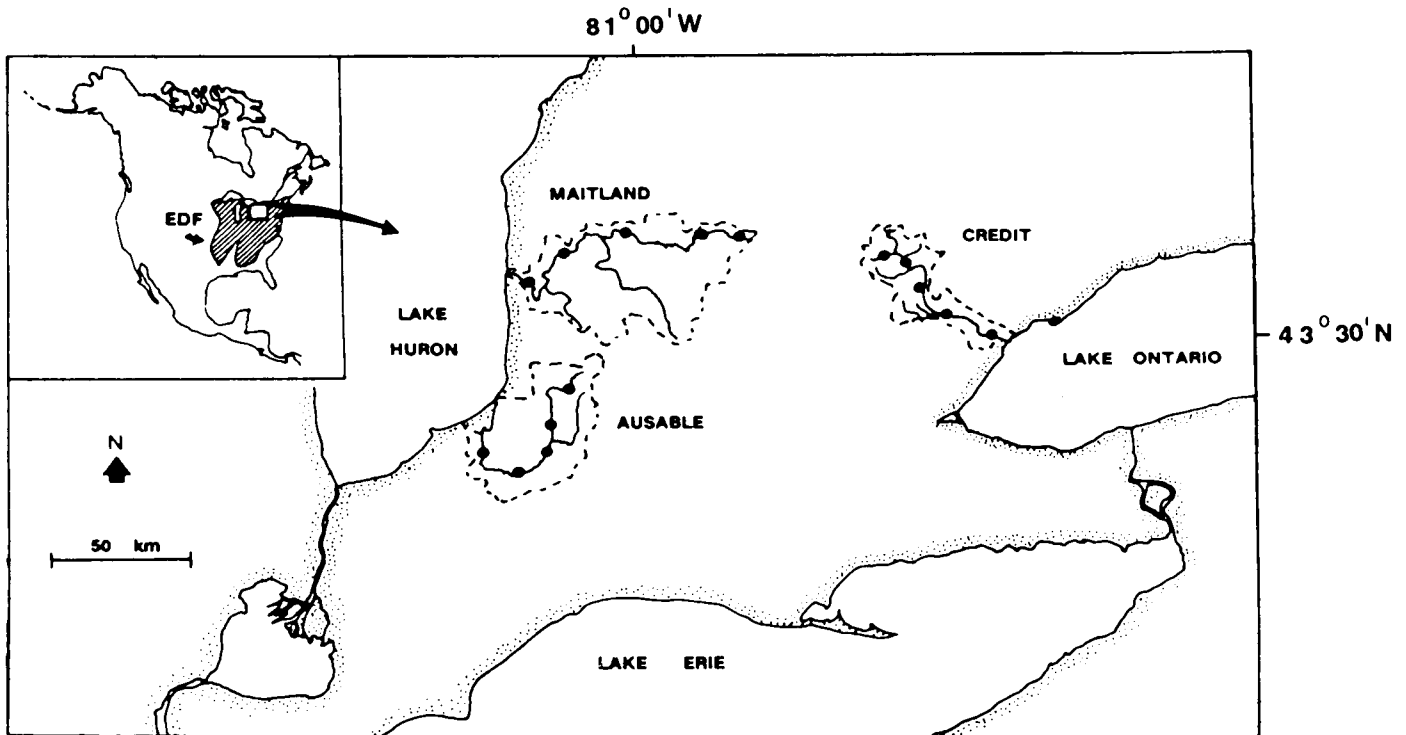


FIG. 1. Map of the Credit, Ausable, and Maitland drainage basins. Sample sites within the basins are indicated by closed circles. The drainage basins are within the eastern deciduous forest (EDF) biome of North America.

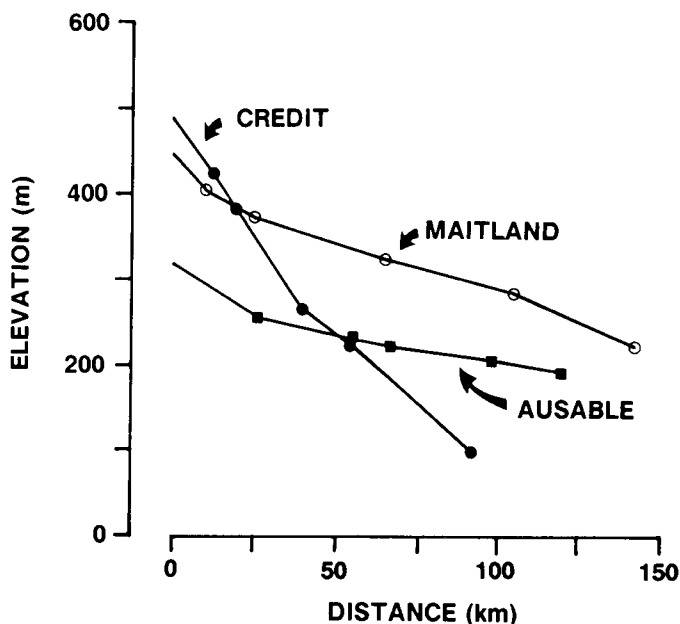


FIG. 2. Longitudinal profiles in terms of elevation and distance from source for the five study site locations on each river (Credit River, closed circles; Maitland River, open circles; Ausable River, closed squares).

retrieved 1 d later to determine the diel range of water temperature.

In situ values for conductivity (Yellow Springs Instrument Co., YSI; model 33), pH (Can Lab digital pH meter, model 607) and dissolved oxygen concentrations (YSI oxygen meter, model 57) were obtained prior to sampling the benthos. Tri-

plicate water samples were collected for analysis of suspended sediments. In the field, a known volume of water was filtered through preweighed, glass fiber GF/C filters and the filters were stored on dry ice. Subsequently, filters (including a control filter wetted with distilled water) were air dried (6 h), oven dried (103°C, 1 h), weighed, ashed (550°C, 20 min) and re-weighed to determine concentrations of suspended sediments (American Public Health Association 1985).

Macroinvertebrate samples were taken using a modified Hess cylinder sampler (0.1 m²) with a 1-m trailing bag (mesh size: 250 µm). Five samples were collected along one transect and preserved with Kahle's fluid (Pennak 1978). In those cases where deep water prevented the collection of samples across an entire channel, samples were taken along two to three partial transects perpendicular to shore. To determine the ash free dry mass (AFDM) of detritus (the particulate organic matter remaining after the animals were retrieved from each sample in the laboratory), samples were air dried for 24 h, oven dried (103°C, 24 h), weighed, ashed (550 ± 25°C, 3 h) and re-weighed.

At each Hess sample point, depth and mean current velocity within the water column were determined (Price Gurley meter during the spring; Ott C2 meter in summer and autumn). Stream width and an overall qualitative assessment of predominant substrate type at river sites were noted. A description of the surrounding land use, riparian vegetation and bank stability, and percent cover or shading over the river also were recorded.

Land use was documented in upstream and downstream directions for as far as I could see. Photographs were taken in upstream and downstream directions at each site in all seasons. I noted any change in vegetation between the river valley and the plateau above. After the first sampling trip, it was clear that

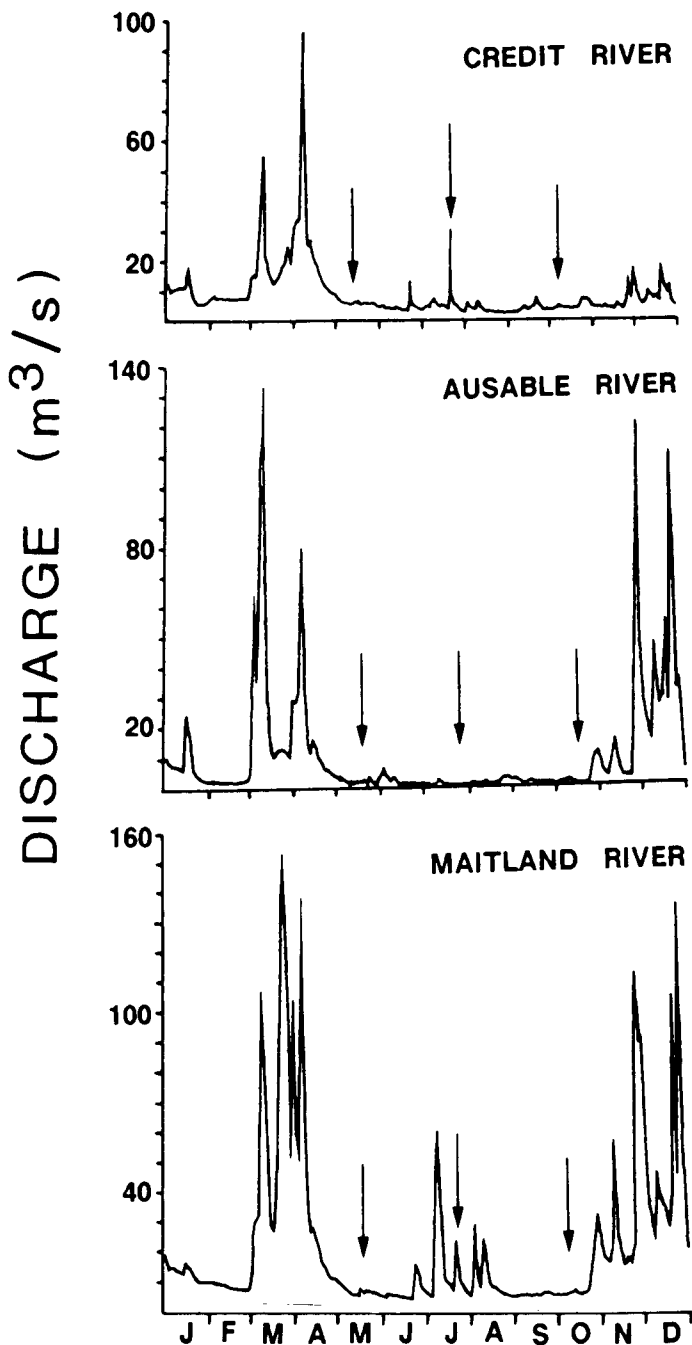


FIG. 3. Discharge data (1987) were provided by the Water Survey of Canada (WSC), Environment Canada, for the most downstream gauging station on each river: Credit River at Erindale (site 5), WSC station no. 02HB002; Ausable River near Springbank (site 4), WSC station no. 02FF002; Maitland River below Wingham (21 km upstream from site 4), WSC station no. 02FE002. The 1987 mean annual flow at each location was 8.98 m³/s (Credit River), 10.4 m³/s (Ausable River) and 20.0 m³/s (Maitland River). Arrows represent sampling dates.

there were three types of land use associated with the study sites selected for study: forested, farmland, and mixed. Mixed land use areas were forested river valleys in farmlands. The 15 river sites were assigned (before macroinvertebrate samples were analysed) to land use types on the basis of these field observations: forested (Credit River sites 1, 2, 3, 4, 5), farmland (Ausable River sites 1, 2; Maitland River sites 1, 2, 3), and mixed (Ausable River sites 3, 4, 5; Maitland River sites 4,

5). One forest site (Credit River site 5) was best described as a forested river valley in an urban locale.

Taxonomic Resolution

Macroinvertebrates can be identified using various biological classifications (size, behaviour, functional feeding group, taxonomic composition) each of which can be related to a set of environmental factors (Corkum and Ciborowski 1988). In this study, I chose to work with taxonomic designations because such categorizations reflect broad environmental requirements as well as the biogeography of constituent groups. However, other biological classifications also could have been used to test the biome dependency hypothesis, recognizing that different categorizations depend on the scale of resolution. For example, some familial classifications correspond well with trophic assignments (e.g. Tricorythidae, Ephemeroptera; all species are collector-gatherers), yet there are problem groups (e.g. Chironomidae, Diptera) in which animals assigned to one familial classification may have representatives belonging to several different trophic levels.

Since distributional patterns of species are a function of biotic interactions, dispersal mechanisms, environmental tolerances and historical factors (Carter et al. 1980), the likelihood of a species being present throughout a large geographical area is low. Earlier, Illies (1961) associated families of aquatic insects with particular river zones (rhithron, potamon) on a world-wide basis. I also chose to compare macroinvertebrate communities among drainage basins using a familial classification.

In the laboratory, each benthic sample was washed through a standard (Tyler®) sieve series (mesh openings: 4.00–0.25 mm). Macroinvertebrates were sorted from the detritus in each size class and identified using a dissecting microscope. Insects were identified generally to familial level. Coarser designations were used for non-insect taxa (Tricladida, Pulmonata, Hirudinea, Branchiobdellida, Oligochaeta, Hydracarina, Amphipoda). Microcrustaceans were not retrieved from samples. Absolute density (number 0.1 m⁻²) was determined for the entire sample.

Data Analyses

A total of 225 macroinvertebrate samples (3 seasons × 3 rivers/season × 5 sites/river × 5 samples/site) was included in the analysis. A replicated, three-way analysis of variance (ANOVA) (Sokal and Rohlf 1981) was used to test for significant differences in macroinvertebrate density (numbers/m²) among rivers, site distances along rivers and seasons.

Ward's hierarchical method of cluster analysis (Wishart 1987) was used to group river collections in all three seasons (45 collections: 15 sites × 3 seasons/site) according to the mean ($n=5$) density of each of 24 dominant taxa. A taxon was considered to be dominant if it accounted for at least 1% of the total density by number of all samples or 1% of any one of the 225 samples.

A series of ANOVA and multiple comparison tests was used to identify taxa that best characterized or defined the collection groupings derived from the cluster analysis. Twenty-four, one-way ANOVA tests (one per dominant taxon) were conducted to detect differences in mean density among the group clusters. If significant differences were observed among group means, a Student–Newman–Keuls (SNK) multiple comparison test was used to determine which group means (if any) did not differ from one another.

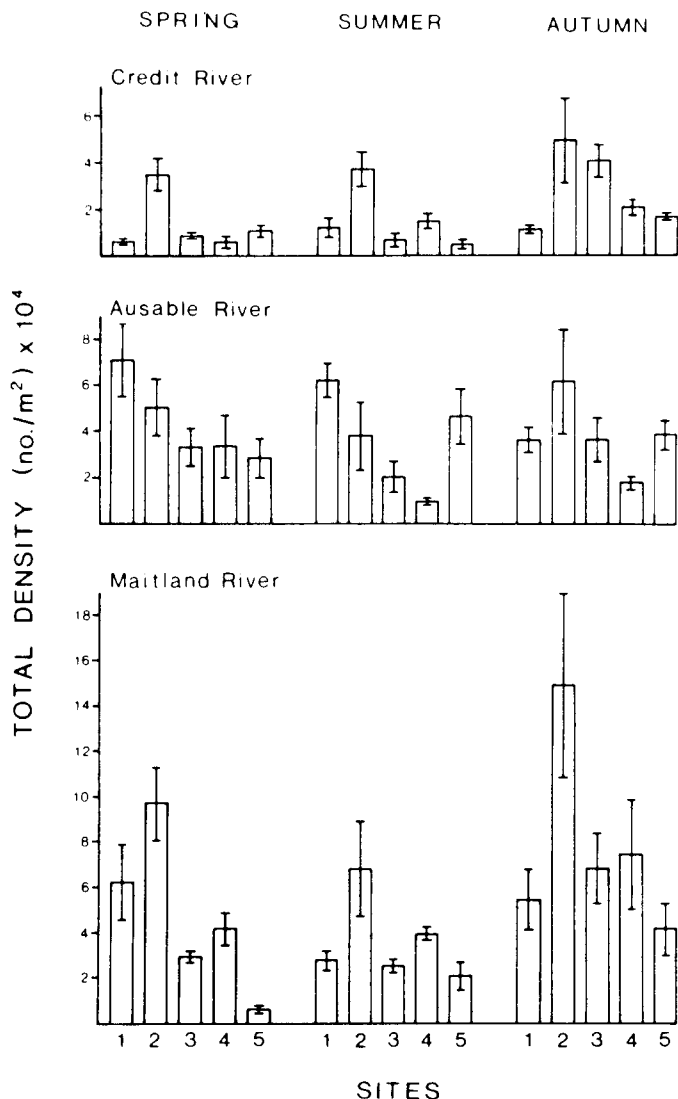


FIG. 4. Mean and standard errors of benthic invertebrate density ($n = 5$ samples) for each of five sites on the Credit, Ausable, and Maitland Rivers in spring, summer, and autumn. Sites are numbered from upstream (site 1) to downstream (site 5) locations.

TABLE 1. Summary of a three-way analysis of variance (ANOVA) test to examine the influence of rivers, site distance along rivers and seasons as well as the interactions of these factors on differences among mean benthic density.

Source of variation	df	SS	MS	F	P
Rivers	2	14.7883	7.3942	17.934	<0.001
Site distance	4	31.2052	7.8013	18.921	<0.001
Seasons	2	54.4733	27.2366	66.060	<0.001
Rivers × Site distance	8	8.8975	1.1122	2.698	<0.01
Rivers × Seasons	4	6.1716	1.5429	3.742	<0.01
Site distance × Seasons	8	23.8593	2.9824	7.234	<0.001
Rivers × Site distance × Seasons	16	18.5328	1.1583	2.809	<0.001
Within group (error)	180	74.2073	0.4123		
Total	224	232.1353			

Multiple discriminant (canonical variate) analysis was used to relate the biological site groupings to the environmental data. This analysis seeks linear combinations of variates that have the greatest between-group variation relative to their within-

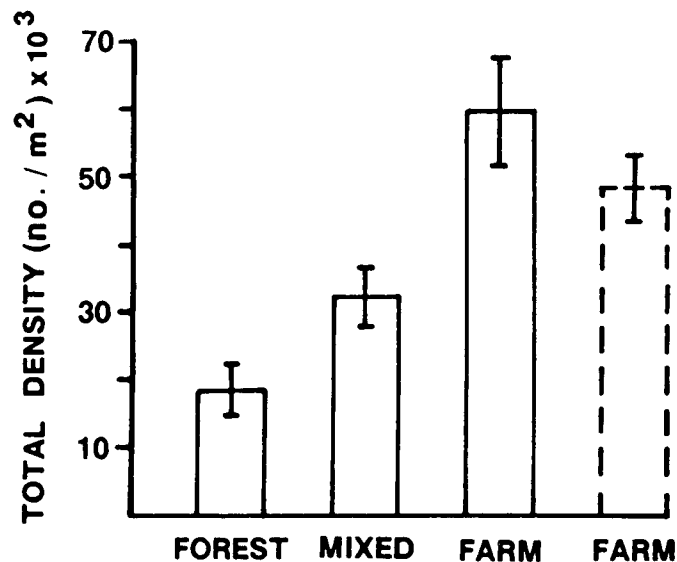


FIG. 5. Mean and standard error of benthic density at river sites for all three sampling seasons associated with the a priori land use designations. The designations were forested (Credit River sites 1,2,3,4,5), mixed (Ausable River sites 3,4,5; Maitland River sites 4,5), and farmland (Ausable River sites 1,2; Maitland River sites 1,2,3). The histogram depicted in dashed lines represents the farming sites excluding all samples from the locally enriched Maitland River site 2.

group variation. The analysis was performed using the statistical package, SPSSX (Norusis 1985).

Results

Macroinvertebrate Density

Significant variability in density was evident among rivers, site locations along rivers, and seasons (Fig. 4, Table 1). Additionally, there were significant interactions among each of these three factors (Table 1). Density was lower at sites on the Credit River than for equivalent sites on the Ausable or Maitland rivers (Fig. 4). Maximum benthic density was recorded at site 2 (downstream from the town of Harriston; population 1884) on the Maitland River. Here, Oligochaeta (worms), Chironomidae (midge larvae), and Tricladida (flatworms) dominated the samples. The prevalence of midges and worms as well as the high benthic density of macroinvertebrates at site 2 reflect local nutrient enrichment from the town.

I also examined mean benthic density for sites associated with forested, farming, and mixed land use areas. Lowest and highest mean densities occurred at sites in forested and farmland areas, respectively, with sites in mixed land use areas having intermediate values (with or without the locally enriched site 2 of the Maitland River) (Fig. 5).

River Site Groupings

The cluster analysis separated the 45 collections (15 sites × 3 seasons/site) characterized by the dominant 24 taxa into three major groups (A, B, C) (Fig. 6). River sites within each group were examined for consistency with respect to sample season, site location along a river, rivers, and adjacent land use (Table 2). Consistency was defined as the maximum number of sites per cluster that fell into one category expressed as a proportion of the total number of sites in that cluster.

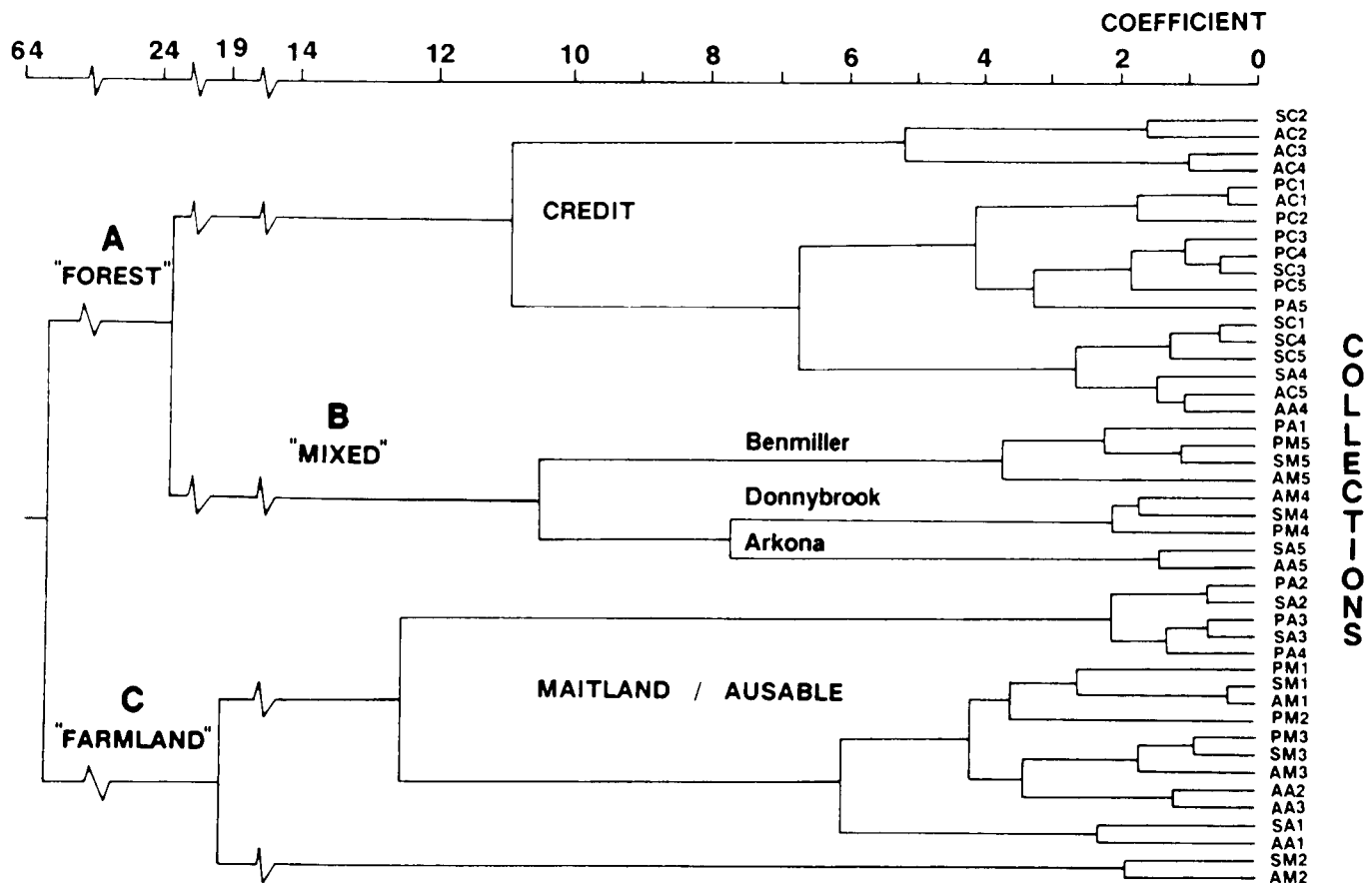


FIG. 6. Dendrogram of 45 collections (3 rivers/season \times 5 sites/river \times 3 seasons/site) was based on Ward's hierarchical cluster analysis for the mean ($n=5$) benthic density of the dominant taxa. Site codes include symbols for season (P, spring; S, summer; A, autumn), river (C, Credit; A, Ausable; M, Maitland) and site locations along the river from 1 (upstream) to 5 (downstream).

An equal number of sites in spring, summer, and autumn occurred in each of the three groups (Table 2). Clearly, sample sites were not grouped according to season.

Next, I examined all combinations of 5 sites sequentially to represent headwaters, mid-reach and downstream areas and compared these designations with the three groups of river sites revealed by cluster analysis. The designation of upstream (sites 1 and 2), mid-reach (sites 3 and 4), and downstream (site 5) regions provided the best fit of any arrangement of between-site locations and the three cluster groups. The highest consistency was between upstream sites and group C (61%). Poorer correspondence was noted between downstream sites and group B (55%) and between mid-reach sites and group A (44%) (Table 2).

Since each river might have a unique assemblage of macroinvertebrates, I also examined the association of the clustered groups with each of the three rivers. Although there was high consistency between Credit River sites and group A (83%), there was poorer correspondence between group B and Maitland River sites (67%) and between group C and Ausable River sites (50%).

There was a high consistency between cluster group membership and a priori land use category. Most sites in forested areas occurred in Group A (83%); sites in mixed areas corresponded well to group B (89%); and sites in farmlands were associated with Group C (78%) (Table 2). Thus, river sites were grouped more consistently according to land use than to site

location along a river, specific river, or to season of collection (Fig. 6).

Macroinvertebrate Assemblages

Benthic densities of the 24 taxa were compared among the three river site groupings (A,B,C) revealed by cluster analysis. Results of 24 ANOVA tests (one per taxon) showed that mean density of Pulmonata, Hydroptilidae, Hydracarina, Simuliidae, and Elmidae did not vary significantly among clusters (Table 3). Significant differences among groups, however, were noted for other taxa. In Table 3, taxa are listed in order of magnitude of their contribution to separation of the river site groups as measured by the ratio of among to within-group variance (F -value). Highest F -values were obtained for mayflies, Caenidae (75.17), and biting midges, Ceratopogonidae (60.03); i.e. these taxa showed the greatest variation among site groupings.

Macroinvertebrate characterization of river site groupings was based on the multiple comparison tests for each taxon in which there were significant differences in benthic density among groups (Table 3). The following macroinvertebrate assemblages characterized the river site groupings each of which was consistently associated with land use type (taxa are listed in order of the magnitude of the F -value): group A "forests" (Hydropsychidae and Leptophlebiidae), group B "mixed" (Heptageniidae, Baetidae, Psephenidae, and Tricorythidae), and group C "farmlands" (Ceratopogonidae, Oligochaeta, Corixidae, and Tricladida). Larvae of Ephemerelli-

TABLE 2. Consistency of season, site location along a river, rivers, and land use areas among the three groups of river sites (A, B, and C) generated by cluster analysis illustrated in Fig. 6.

Season				
Grouping	Spring	Summer	Autumn	Consistency
A	6	6	6	0.33
B	3	3	3	0.33
C	6	6	6	0.33

Site Location				
Grouping	Upstream (sites 1,2)	Midstream (sites 3, 4)	Downstream (site 5)	Consistency
A	6	8	4	0.44
B	1	3	5	0.55
C	11	7	0	0.61

River				
Grouping	Credit	Ausable	Maitland	Consistency
A	15	3	0	0.83
B	0	3	6	0.67
C	0	9	9	0.50

Land Use				
Grouping	Forested	Mixed	Farmland	Consistency
A	15	3	0	0.83
B	0	8	1	0.89
C	0	4	14	0.78

dae and Plecoptera were most prevalent in both "forested" and "mixed" land use groupings of river sites. Seven taxa (Caenidae, Coenagrionidae, Amphipoda, Sphaeriidae, Branchiobdellida, Chironomidae, and Hirudinea) were characteristic of those river sites in both "mixed" and "farmland" areas. Since branchiobdellids are always associated with crayfish (Pennak 1978), one would also expect crayfish occurrence in mixed and farmland river sites. No taxon had similarly high densities at river sites in both "forested" and "farmland" areas.

Environmental Variables

Values of environmental variables were examined for sample collections within each of the groupings generated using cluster analysis (Table 4). Results of one-way ANOVA tests for equality of mean values of continuous environmental variables showed that there were significant differences in AFDM ($P < 0.01$), river width ($P < 0.005$), and mean current velocity ($P < 0.001$) among the three cluster groups that were consistently associated with land use areas. Results of the SNK multiple comparison tests indicated that AFDM at river sites in group B "mixed" and C "farmland" areas were not significantly different from one another; values of AFDM in these groupings were greater than in group A "forested" river sites. No differences in river width were discerned between Group A or C sites; widest river sites were in group B, the "mixed" land use area. Mean current velocity differed significantly among the three groups. Group C sites had the slowest-flowing water and group A river sites had the fastest-flowing water; sites in group B had intermediate values of current velocity. Since sampling depth was limited by the height of the Hess sampler

(55 cm), the lack of significance in depth variation among groups should be treated with caution.

Discriminant (canonical variate) analysis was used to determine which independent environmental variables best separated river sites within the three groups revealed by cluster analysis. The first two functions were significant in discriminating among the three groups of river sites (Table 5). The overall success rate for sites correctly predicted using the set of environmental variables was 95.6%. All river sites in group A "forested" areas were correctly classified. One group B collection (PA1, spring Ausable River, site 1) was misclassified with group C. One group C collection (SM3, summer Maitland River site 3) was misclassified with group B (Fig. 6 and 7).

Figure 7 shows the separation of the three groups on the first two discriminant functions (DF1 and DF2). DF1 explained 86% of the variation among the three groups (Table 5). In function 1, mean current velocity and AFDM of benthic detritus exhibited the highest positive and negative correlations, respectively (Table 5). Mean current velocity was highest and AFDM of detritus was lowest at river sites in group A "forested" areas (Fig. 7). In contrast, mean current velocity was lowest and AFDM of detritus was highest at river sites in group C "farmland" areas. River sites in group B "mixed" areas had intermediate values of these environmental variables.

The second discriminant function explained an additional 14% of the variability among groups (Table 5). River width was the major environmental variable that accounted for the separation of sites in group B from the other two groups on the second discriminant function. Rivers were wider at sites in group B "mixed areas" than at sites in either A "forested" or C "farming" areas.

Discussion

The present study was designed to test for biome dependency by determining whether or not macroinvertebrate communities were comparable at sites among drainages within the same biome regardless of site location along a river. My study results did not support the biome dependency hypothesis. Contrary to predictions, macroinvertebrate assemblages and total density of the benthos differed among river sites in the eastern deciduous forest (EDF) biome. Moreover, community composition did not vary consistently among drainages, with site distance from river source or with season. Instead, macroinvertebrate composition and total density of the benthos was associated with the type of land use adjacent to the sample site.

Although relationships between biotic and abiotic factors along rivers have been well documented in north temperate regions (Power et al. 1988), the surrounding vegetation of the rivers that I studied did not follow the continuum model (Vannote et al. 1980) of forested headwaters (with the associated input of autumnal leaf fall) typically used to describe EDF drainage basins. The headwaters of the Ausable and Maitland rivers originated in farmlands, and flowed into forested river valleys. Deciduous forests were prevalent at all river sites sampled along the Credit.

In this study, the different types of land use were not apportioned equitably among the three drainage basins. Clearly, additional field tests are needed to examine the influence of land use "blocked" at different locations within drainage basins. Despite this limitation, my results revealed a strong correspondence between type of land use and benthic density as well as macroinvertebrate assemblages at river sites.

TABLE 3. Density of benthic invertebrates among three river site groupings (A, B, C) revealed by cluster analysis (Fig. 6). A one-way ANOVA was performed on each of 24 taxa to determine whether significant differences occurred in mean density of a taxon among groups. Data were transformed $[\ln(x + 1.1)]$ prior to analysis. The taxa are listed in order of the magnitude of their contribution to the groups as measured by the *F*-value (ratio of among-group to within-group variance). N.S. = not significant. Student–Newman–Keuls multiple comparison tests were used to compare means for each taxon. Groups linked by lines are not significantly different from one another.

Taxon	<i>F</i> (2,42)	<i>P</i>	Density (mean ± SE) of macroinvertebrates (number per 0.1 m ²)		
			A "Forest" (18 sites)	B "Mixed" (9 sites)	C "Farmland" (18 sites)
Caenidae	75.17	<0.001	2.3 (0.8)	153 (38)	264 (67)
Ceratopogonidae	60.03	<0.001	0.5 (0.4)	4.8 (1.8)	53 (19)
Heptageniidae	28.21	<0.001	29 (8)	84 (13)	5.7 (1.8)
Hydropsychidae	25.37	<0.001	107 (27)	32 (20)	3.4 (1.9)
Oligochaeta	20.25	<0.001	334 (92)	1025 (414)	2179 (346)
Baetidae	19.64	<0.001	111 (30)	371 (139)	18 (9)
Psephenidae	16.08	<0.001	1.1 (0.5)	11 (3)	4.0 (1.1)
Coenagrionidae	15.86	<0.001	0.5 (0.4)	5.4 (2.5)	10 (3)
EphemereIIDae	14.79	<0.001	90 (45)	59 (37)	0.6 (0.4)
Corixidae	12.00	<0.001	0	0.8 (0.7)	29 (12)
Tricorythidae	11.38	<0.001	13 (5)	174 (71)	0.7 (0.6)
Amphipoda	11.02	<0.001	1.9 (1.0)	35 (12)	33 (8)
Plecoptera	9.43	<0.001	17 (7)	22 (19)	0.6 (0.4)
Tricladida	8.17	<0.005	6.7 (3.8)	4.9 (1.8)	133 (97)
Sphaeriidae	5.19	<0.025	1.8 (0.5)	9.0 (4.8)	39 (25)
Leptohlebiidae	5.18	<0.01	9.3 (4.1)	1.0 (0.7)	0.5 (0.4)
Branchiobdellida	5.02	<0.025	2.4 (1.6)	15 (11)	30 (11)
Chironomidae	4.71	<0.025	853 (148)	1693 (369)	1796 (351)
Hirudinea	4.65	<0.025	0.0 (0.0)	1.9 (1.2)	5.7 (3.9)
Pulmonata	3.17	N.S.	5.1 (2.6)	22 (10)	102 (67)
Hydroptilidae	2.73	N.S.	25 (8)	120 (47)	79 (57)
Hydracarina	2.21	N.S.	40 (15)	124 (72)	72 (15)
Simuliidae	1.69	N.S.	13 (9)	36 (22)	20 (19)
Elmidae	0.22	N.S.	100 (33)	110 (32)	151 (52)

TABLE 4. Comparison (mean ± SE) of the continuous environmental variables among the three river site groupings (A, B, C) generated by cluster analysis (Fig. 6). One-way ANOVA tests were used to determine significant differences in mean values of environmental variables on transformed data $[\ln(x + 1)]$ among the groups. Student–Newman–Keuls multiple comparison tests were used to compare means for each variable. Groups linked by lines are not significantly different from one another.

Variable (units)	<i>F</i> (2,42)	<i>P</i>	A "Forest" (18 sites)	B "Mixed" (9 sites)	C "Farmland" (18 sites)
Ash free dry mass (g/0.1 m ²)	5.91	<0.01	1.173 ± 0.182	2.283 ± 0.580	2.421 ± 0.303
Suspended sediments (mg/L)	2.37	NS	6.8 ± 3.0	1.6 ± 0.4	3.0 ± 0.8
Minimum water temperature (°C)	0.17	NS	14.4 ± 1.4	16.0 ± 2.4	15.5 ± 1.6
Maximum water temperature (°C)	0.17	NS	19.1 ± 1.5	20.0 ± 2.7	21.0 ± 1.9
pH (pH)	1.81	NS	8.2 ± 0.07	8.3 ± 0.05	8.1 ± 0.06
Conductivity (µS/cm, 25°C)	0.38	NS	401 ± 11	423 ± 24	412 ± 12
Dissolved oxygen (mg/L)	0.70	NS	8.5 ± 0.6	8.6 ± 0.8	7.8 ± 0.8
River width (m)	6.83	<0.005	16.3 ± 1.4	47.2 ± 11.3	19.9 ± 2.8
Mean depth (cm)	0.34	NS	26.2 ± 2.3	28.8 ± 3.3	29.4 ± 2.8
Mean current velocity (m/s)	41.09	<0.001	0.514 ± 0.041	0.301 ± 0.041	0.064 ± 0.022

There is a strong association between stream characteristics and the surrounding land (Hynes 1975). Moreover, land use type is linked to the topography. For example, farms in the

study area are on flat or gently rolling terrain; forests are often on hilly flood plains. Typically, more nutrients are released into receiving waters from croplands than from forested areas (Lik-

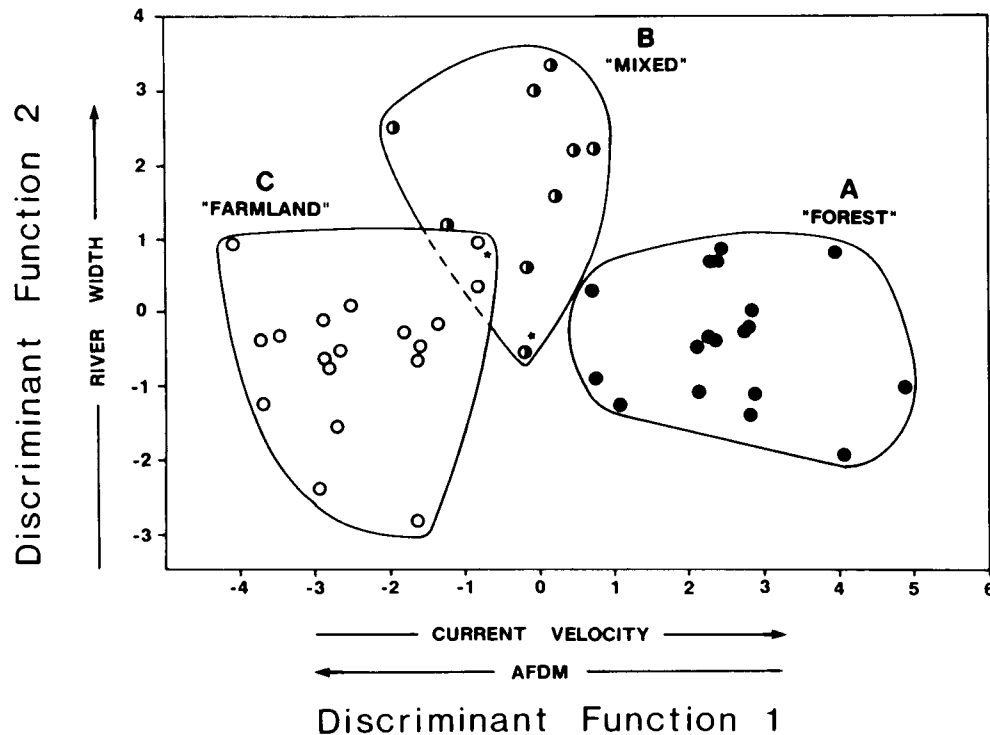


FIG. 7. Separation of river sites into group A "forested" (closed circles), group B "mixed" (half closed circles), and group C "farmland" (open circles) areas using the first two discriminant functions. Lines enclose all sites for each of the three groups. * = misclassified sites in the analysis (see text). Current velocity, ash free dry mass (AFDM), and river width are the factors most useful in delineating site groupings.

TABLE 5. Standardized canonical discriminant coefficients of environmental variables (coeff) and pooled within group correlations (corr) between variables and canonical discriminant functions.

Variable	Function 1		Function 2	
	coef	corr	coef	corr
Mean current velocity	1.025	0.69	0.087	0.20
Bank stability	0.123	0.34	0.064	0.29
Substrate	0.270	0.19	0.194	0.23
Cover	-0.116	0.12	-0.101	-0.29
Suspended sediments	0.165	0.08	-0.636	-0.30
pH	0.112	0.08	0.000	0.25
Dissolved oxygen	0.081	0.07	-0.009	0.10
Minimum water temperature	-0.776	-0.03	1.134	0.07
Maximum water temperature	0.643	-0.04	-0.952	-0.02
River width	-0.188	-0.04	0.955	0.60
Conductivity	-0.319	-0.04	0.244	0.12
Mean depth	-0.028	-0.05	-0.558	0.05
Ash free dry mass	-0.760	-0.22	0.192	0.14
X ² (df) after each function	88.82 (26)		22.45 (12)	
Probability	<0.001		<0.03	
Variance explained (%)	86.0		14.0	

ens and Bormann 1974). Although I did not obtain direct measures for algal productivity, values of detrital AFDM (an indirect measure of production) were higher at sites in farmland and mixed areas than at sites in forested areas. River sites associated with farmland were slower-flowing, exhibited higher levels of detritus and benthic macroinvertebrate density than the faster-flowing river sites on steeper slopes of forested regions (Fig. 2 and Table 4).

Riparian vegetation controls to a large extent the rates at which sediments and nutrients enter receiving rivers (Johnson

et al. 1969; Schlosser and Karr 1981). Peterjohn and Correll (1984) showed that most nutrients from agricultural lands are intercepted by riparian forests before entering receiving waters. Thus, land use within the drainage basin influences the productivity of receiving waters and the rate of transfer of materials and energy can be altered by the characteristics of streamside vegetation.

Despite the strong association between water quality of rivers and the associated landscape reported in the literature, the link between riverine fauna and the landscape is less clear. Density and biomass values of benthic macroinvertebrates are often greater in open, unshaded areas than in forested reaches with overhanging canopies, reflecting potential differences in abundance and production of benthic primary producers (Cummins 1975b). Erman et al. (1977, cited in Gregory 1983) showed a similar relationship in clearcut and forested river sites in California. There, wide (30 m) buffer strips provided shade and resulted in a decrease in benthic abundance. Other workers (Woodall and Wallace 1972; Molles 1982) have also demonstrated a correspondence between some aspect of the macroinvertebrate community and vegetation type within drainage basins. These results are consistent with the present study in which macroinvertebrate density at sites in mixed land use areas was intermediate between high levels at sites in farmlands and low levels at sites in forests (Fig. 5).

Ward (1989) conceptualized lotic systems in terms of four-dimensional axes (longitudinal, lateral, hyporheic, and temporal). In this study, macroinvertebrate assemblages corresponded more consistently with land use areas (terrestrial vegetation away from the river channel) than with either longitudinal (upstream/downstream) or temporal (seasonal) dimensions. The most consistent fit between the longitudinal

dimension and the three clusters of sites was obtained because upstream sites occurred in farmlands.

The macroinvertebrate composition at sites along rivers was independent of sample season. It is not unusual to expect that most taxonomic families would be present throughout the year within the limited geographic range examined. Coarser taxonomic designations mask the seasonal life history patterns characteristic of many species (Hynes 1970).

Because workers have had difficulty in applying empirically derived relationships developed in one river to other waterbodies (Hawkes 1975), one might consider that each river maintains a unique assemblage of invertebrates. This was not the case. Although the Credit River sites in the deciduous forest basin comprised 83% of one river grouping, the correspondence between site groupings and the Ausable and Maitland rivers was lower (Table 2, Fig. 6).

Proponents of the river continuum concept suggested that a strong link existed between riparian vegetation, the relative proportion of allochthonous and autochthonous matter, and feeding groups of stream insects along the length of rivers (Vannote et al. 1980; Cummins et al. 1984). Other workers (Winterbourn et al. 1981; Miller 1985; Hawkins 1988) have been unable to substantiate the proposed relationship between riparian vegetation and invertebrate feeding guilds. Wiggins and Mackay (1978) found that functional feeding groups of caddisflies differed between eastern deciduous forest and western montane forest biomes. The ratio of shredders to grazers in headwater regions of rivers differed between eastern deciduous (3:2) and western montane (1:1) biomes, suggesting that resource availability for grazers was greater in the west than the east (Wiggins and Mackay 1978). Thus, vegetational differences among biomes, land use areas nested within biomes, and the modifying effects of riparian vegetation are all factors to be considered in the prediction of distributional patterns of lotic macroinvertebrate assemblages.

I was able to distinguish characteristic macroinvertebrate assemblages for groups of river sites associated with different types of land use. Hydropsychid caddisflies and the leptophlebiid mayflies were most characteristic of "forested" sites with the highest mean current velocities and lowest levels of detrital AFDM in the samples. Hydropsychids are collector-filterers and/or predators; leptophlebiids are collector-gatherers or shredders. Both taxa cling to rocky substrates in lotic erosional areas (Ross 1963; Merritt and Cummins 1978). Although shredders are most often associated with forested headwater streams of EDF (Vannote et al. 1980), leptophlebiid larvae occurred along the upper 40 km of the forested drainage basin of the Credit. This suggests that surrounding vegetation may modify community composition in rivers in ways other than simply providing an energy source.

The assemblage of invertebrates at "mixed" river sites included scrapers (psephenids and baetids) and collector-gatherers (baetids, tricorythids, and heptageniids). All of these organisms cling to the substrate; baetids also may swim within the water column. All can typically be found in both lentic and lotic erosional sites; baetids and tricorythids also may occur in lotic depositional areas. These habitats were common at river sites within the mixed land use areas.

In contrast to many rivers where predators seldom account for more than 10% of the fauna at any one location and their relative abundance does not change longitudinally (Cummins 1975b; Vannote et al. 1980), the "farmland" river sites in this study were characterized by numerous predators. The charac-

teristic fauna of farmland sites were ceratopogonids (predators or collector-gatherers), corixids (collector-gatherers and/or carnivores), oligochaetes (omnivores) and triclads (predators). These organisms crawl (oligochaetes, triclads) or sprawl (ceratopogonids) on riverbeds of depositional areas. Whereas ceratopogonids may swim into the water column, corixids dwell there. In this study, high nutrient levels (fertilizers) at farmland sites could account for a high turnover of species or the presence of multivoltine species that would support numerous macroinvertebrate predators. In addition, invertebrate predators are often abundant in areas devoid of fish (Macan 1977).

In summary, I have shown that there is a strong correspondence between type of land use and macroinvertebrate assemblages in rivers within a biome. Terrestrial vegetation away from the river channel (the lateral dimension) exerted a stronger influence on macroinvertebrate assemblages at river sites than factors associated with the longitudinal gradient. With changes in characteristic vegetation in the deciduous forest biome, there was a corresponding change in the lotic macroinvertebrate community. Study results were not consistent with the biome dependency model largely because the vegetation that characterized the biome had been disturbed. The "mixed" land use group of river sites (forested river valleys within farmland communities) revealed by cluster analysis was faunistically more similar to river sites in "forests" than in "farmlands." It would be useful to know how wide a buffer strip must be in relation to channel width to induce a shift in characteristic macroinvertebrate assemblages from a "mixed" to a "forested" area.

Perhaps macroinvertebrate assemblages that characterize enriched river sites in farmlands can be reset to reflect presettlement (i.e. forested) conditions by modifying the landscape adjacent to river sites. The faunal similarity between "mixed" and "forested" river groupings as well as the intermediate levels of benthic density at mixed sites between low density levels at forested sites and high levels at farmland sites suggest that such a resetting of the lotic macroinvertebrate community is possible.

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